SHOUT
SHARE
IT

HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

BULLETIN

OF THE

MUSEUM OF COMPARATIVE ZOOLOGY

AT

HARVARD COLLEGE, IN CAMBRIDGE

VOL. 115

CAMBRIDGE, MASS., U. S. A.
1956-1957

The Cosmos Press, Inc.
Cambridge, Mass., U.S.A.

CONTENTS

PAGE

No. 1.—Notes on American Earthworms of the Family Lumbricidae. III-VII. By G. E. Gates. August, 1956 1

No. 2.—A Quantitative Study of the Equidae of the Thomas Farm Miocene. By Robert S. Bader. August, 1956 47

No. 3.—*Aneuretus simoni* Emery, a Major Link in Ant Evolution. By E. O. Wilson, T. Eisner, G. C. Wheeler and J. Wheeler. (3 plates.) August, 1956 79

No. 4.—The Types of Naiades (Mollusca: Unionidae) in the Museum of Comparative Zoology. By Richard I. Johnson. September, 1956 . . . 99

No. 5.—Pseudemys scripta callirostris from Venezuela with a General Survey of the scripta Series. By Ernest Williams. (3 plates.) September, 1956 143

No. 6.—Revision of the African Tortoises and Turtles of the suborder Cryptodira. By Arthur Loveridge and Ernest E. Williams. (18 plates.) February, 1957 161

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 115, No. 1

NOTES ON AMERICAN EARTHWORMS OF THE FAMILY LUMBRICIDAE. III-VII.

By G. E. Gates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM

August, 1956

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 115.

Breviora (octavo) 1952 — No. 57 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899-1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 1

NOTES ON AMERICAN EARTHWORMS OF THE FAMILY LUMBRICIDAE. III-VII.

By G. E. Gates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
August, 1956

No. 1 — *Notes on American earthworms of the family Lumbricidae.* III-VII.

By G. E. Gates

III

Bimastos tumidus (Eisen, 1874)

Allolobophora tumida Eisen 1874, Öfv. Vet. Ak. Förh., 31, p. 45. (Type locality, Mt. Lebanon, New York-Massachusetts. Type, one half of anterior end sagittally sectioned by Smith, in U. S. Nat. Mus.)

Allolobophora gieseleri Ude 1895, Zool. Anz., 18, p. 339, Zeit. wiss. Zool., 61, p. 127. (Type locality, Savannah, Georgia. Types, numerous, in Hanover Provincial Mus.?)

Allolobophora (*Bimastus*) *tumida* + *A.* (*B.*) *gieseleri*, *Helodrilus* (*B.*) *t.* + *H.* (*B.*) *g.*, Michaelsen, 1900, Abh. Nat. Ver. Hamburg, 16, p. 16, Das Tierreich, 10, p. 502.

Helodrilus gieseleri hempeli Smith 1915, Bull. Illinois Sta. Lab. Nat. Hist., 10, p. 551. (Type locality, Havana, Illinois. Types in U. S. Nat. Mus.)

Helodrilus (*Bimastus*) *tumidus* + *H.* (*B.*) *gieseleri* f. *typica* + *H.* (*B.*) *gieseleri* var. *hempeli*, Smith, 1917, Proc. U. S. Nat. Mus., 52, pp. 170-172.

?

Bimastus ducis Stephenson 1933, Proc. Zool. Soc. London, 1932, p. 939. (Type locality, Durham, North Carolina. Holotype in Brit. Mus.)

Tamalpais, Marin County, California, 0-0-1 (macerated). California Ac. Sci.

New Orleans, Louisiana. Under logs in moist river bottom forest, Dec. 31-Jan. 1, 1931-32, 0-1-0. J. M. Valentine per Dr. G. E. Pickford.

Big Thicket, Texas, May 1, 1938, 0-0-1. Ottys Sanders.

Athens, Texas. Six miles to the north, April 3, 1948, 0-0-3. Ottys Sanders.

Paris, Texas. Eleven miles to the south, March 29, 1952, 0-0-1. Ottys Sanders. (Three specimens, without label, from Mr. Sanders probably also from Texas.)

North Dublin, Virginia. Sawdust, Little Walker Creek, June 25, 1955, 0-2-17. Prof. Walter Harman.

South Rushton, Louisiana. In and near ash of sawdust pile, April 2, 1955, 0-0-3. Prof. Walter Harman.

Lincoln Parish, Louisiana, March 10, 1955, 0-0-2. Bobby Wise per Prof. Walter Harman.

External characteristics. Length, 26-40 mm. Diameter, 2-3.5 mm. Segments, 81-122 (cf. Table 1). Anal segment of worms not recently amputated usually longer than penultimate one and with setae in middle of anterior half but with little or no indication of a dorsal pore or an intersegmental furrow that would mark off setigerous portion into a metamere. Body approximating to four-sided posteriorly, the dorsum slightly rounded and wider than the ventrum, one setal couple at each corner. Pigmentation (unrecognizable in alcoholics except at site of clitellum in a Louisiana worm) red, in dorsum, reaching ventrally to or nearly to *B* through most of axis, also present in ventrum of some or all of first fourteen segments, lacking at intersegmental furrows, in wide transverse stripes in clitellar segments (recently preserved Virginia worms). Prostomium epilobous, tongue open (all). Setae begin on ii on which all usually are present, paired but not as closely as in some lumbricids, *d* about at mL anteriorly but more dorsal posteriorly where *CD* a trifle$<AB$, $BC<AA$, $DD<\frac{1}{2}$C but$>AA$. Nephropores, recognizable only on a few segments, just above *B* on xv (all worms on which pores of that segment were recognizable), on clitellum irregularly and sometimes asymmetrically alternated between levels just above *B* and well above *D* (Virginia). Possible sites on more anterior segments have been noted on several specimens after some softening and removal of the cuticle; at or above *D* on iii-vi, slightly above *B* on vii-ix, above *D* on xi. First dorsal pore on 5/6 (all).

Female and male pores equatorial and at usual levels on xiv and xv respectively. Male pore tumescences in median half of *BC*, confined to xv but sometimes dislocating 14/15 and 15/16 slightly, occasionally reaching on one or both sides slightly into xvi.

Clitellum saddle-shaped, reaching ventrally nearly to *B* (Louisiana) or to *A*, located as follows; xx-xxix (1, Louisiana), xx-xxx (2, Texas), (xx-xxi?) xxii-xxix (2, Texas), (xxi?) xxii-xxix (1, Texas), posterior part/xxi-anterior part/xxx (1, Virginia), (xxi?) xxii-xxx (1, Louisiana), xxii-xxix (14, Virginia and 4, Louisiana), xxii-xxix and onto xxx (2, Virginia), xxii-xxix and possibly xxx (2, Texas), xxii-xxx (3, Virginia, Texas and California). Tubercula pubertatis lacking.

Genital tumescences lacking or unrecognizable.

Internal anatomy. No septa thickly muscular. Longitudinal musele band at mD with pigment, scattered flecks of red pigment present on (in or under?) peritoneum of dorsum anteriorly (10, Virginia).

Calciferous gland extends well into x, the posterior portion of the gut in that segment often with an appearance as of a pair of vertieal saes. Gland of about the same calibre through xi-xii, unconstricted at insertion of 11/12. Intestinal origin in xv (24). Gizzard in xvii-xviii (24). Typhlosole begins gradually in region of xxi and in places may reach floor of gut, slightly widened ventrally in an anterior portion and there with a single median groove. The typhlosole ends abruptly as shown in the table.

Subneural trunk unrecognizable (22), very narrow but in part red and on ventral face of cord (2). Extra-oesophageal trunks empty, apparently passing into dorsal trunk posteriorly in xii (1, Virginia). Hearts present in vii-xi, those of vii empty in two worms (Virginia). Nephridial ducts, at least behind xv, pass into parietes at *B*. Vesicle, U-shaped.

TABLE 1

Typhlosole termination and segment number in *Bimastos tumidus*

Typhlosole ends in segment	Atyphlosolate segments	Number of segments		Remarks
81	19	100		Posterior amputee
83	17	91	*	Posterior amputee ?
85	15	100		Posterior amputee ?
95	20	115		
97	16	113	* 2.	Posterior amputees?
97	20	117		Louisiana
98	19	117		Posterior amputee ?
99	12	111	*	Posterior amputee ?
101	13	114	*	Posterior amputee ?
103	15	118		Louisiana
106	16	122		Louisiana
107	15	122		Louisiana

* Last segment with setae as indicated on page 1.
All worms from Virginia except as otherwise indicated.
Segment number of other worms: 81 (posterior amputee), 107 (posterior amputee), 108, 113, 120.

Seminal vesicles rather small, two pairs, in xi-xii (24). Male funnels crenellate (24). Male deferent ducts slender, shortly looped just behind funnel septa, the loops crowded into a small, leaf-shaped disc. The ducts of a side come into contact in xii where they apparently unite. They disappear from sight at anterior margin of atrial gland or are recognizable further posteriorly on surface of the gland (24). The ducts must have grown posteriorly to or nearly to eq/xv, in some of these worms, before the developing atrial gland had penetrated through the longitudinal musculature. Spermathecae lacking (24). Ovisacs of about the same size as the ovaries and slightly lobed (24).

Atrial gland crossed in xv by an equatorial cleft, a second cleft possibly at insertion of 15/16 as the gland seems to extend slightly into xvi. No glands on parietes in *BC* of clitellar segments nor in association with setal follicles. No setal follicles especially protuberant into coelom (no genital setae?) in fourteen Virginia and Louisiana worms.

Abnormality. Spiral metamerism involving v-vi only (1, Virginia). Metameric abnormality in preanal region (1, Virginia).

Life history. Slight iridescence was recognizable on each male funnel in ten Virginia worms collected on the 25th and 27th of June, as well as in four from Louisiana (March 10 and April 2). Male deferent ducts also appeared to be slightly iridescent. No spermatophores. Seminal vesicles of an aclitellate Virginia worm were of the same small size as in clitellate specimens and had small brown bodies near dorsal ends, but none of the usual external indications of postreproductive regression was recognized. The clitellum of some Virginia and five Louisiana worms may have been at maximal tumescence. Sparse sperm production apparently is indicated by these worms, in which case uniparental reproduction perhaps should be anticipated, possibly parthenogenesis.

Parasites. Cysts, in coelomic cavities of anterior half of body of a Texas worm, are attached to parietes and septa by long filaments.

Remarks. Condition of the author's worms (most of them alcoholic) is fair to very poor; the softened body wall of the California worm was already broken through before removal

from the tube in which it arrived. Much better material was, however, loaned by Prof. Harman, a favor which is much appreciated.

Spermathecal vestiges were not recognizable in the parietes after removal of longitudinal musculature but broad transverse bands of pigmentation became quite obvious.

Septa 6/7 or 7/8 to 11/12 or 14/15 are somewhat strengthened but none is thickly muscular. The thickness seems to vary with the contraction or relaxation of the worm at preservation as well as with degree of maceration. Differences detectable in dissection, insofar as present material is concerned, are slight and do not appear to be of any taxonomic value.

Function and phylogeny of the gland present on the parietes over site of male pore and its tumescences in many lumbricids are unknown. The characterization "atrial" is retained, for want of a better term, but without any connotations as to function or evolutionary history.

The clitellum of one Texas worm was about as in *tumidus,* of two as in *gieseleri,* of another as in *hempeli.* The differences appear to be no greater than are now to be expected in normal intraspecific variation.

B. ducis, known only from the original description of the type, was thought to be distinguished, presumably from *tumidus* and *gieseleri,* by a longer clitellum of 11½ segments. The last hearts of *ducis* are in x, according to Stephenson, but hearts of xi when empty may not be readily recognizable in ordinary museum material. Number of chambers in the calciferous gland, which Smith (1917) believed to be of taxonomic importance (though he did not always mention them) is unknown.

The clitellum covers 8-11 segments in *tumidus* and another half segment may be within the range of normal intraspecific variation in *Bimastos.* Location of anterior boundary of the clitellum, at or in front of 21/22, also characterizes *tumidus* but no other species of *Bimastos.* Coverage of xxxi-xxxii by the clitellum now seems to be the only reason that can be cited in support of retention of *ducis.*

B. longicinctus Smith and Gittens 1915 has a clitellum, in Illinois, according to its authors, of 10-11 segments, on xxiii-xxxii or xxxiii. Location in worms subsequently recorded by others from Ohio and Arkansas without data as to variation presumably

was the same, as the organ is all that enables routine identification of the species. Number of segments covered is about the same as in *tumidus,* but the anterior margin is at 22/23 rather than at 21/22 or anteriorly. The only other method available for separating these two forms involves counting chambers or partitions in the calciferous gland. There are about 60 of these in *longicinctus,* about 40 in *tumidus.* The difference, according to Smith (1917, p. 175), is sufficient to warrant specific distinction. Although little is known as yet about variation in such a character, requiring microtome sections, the number of partitions in the calciferous gland of *Eisenia rosea* (Savigny, 1826) is 38-54.

IV

Bimastos parvus (Eisen, 1874)

Allolobophora parva Eisen 1874, Öfv. Vet. Ak. Förh., 31, p. 36. (Type locality, Mt. Lebanon, New York-Massachusetts. Types in U. S. Nat. Mus.)

Allolobophora beddardi Michaelsen 1894, Zool. Jahrb. Syst., 8, p. 182. (Type locality, Orlando, Florida. Type in Hamburg Mus.?)

Allolobophora (*Bimastus*) *parva* + *A.* (*B.*) *beddardi, Helodrilus* (*B.*) *p.* + *H.* (*B.*) *b.,* Michaelsen, 1900, Abh. Nat. Ver. Hamburg, 16, pp. 14-13, Das Tierreich, 10, p. 502.

Helodrilus (*Bimastus*) *parvus* + *H.* (*B.*) *beddardi,* Smith, 1917, Proc. U. S. Nat. Mus., 52, p. 173.

Bimastus parvus + *B. beddardi,* Kobayashi, 1940, Sci. Rep. Tohoku Univ., 15, pp. 297, 298.

Bimastus beddardi, Cernosvitov and Evans, 1947, Linnean Soc. London, Synopses British Fauna, 6, p. 18.

Mexico. In soil around roots of plants from Guadalajara, Jalisco, in baggage arriving at Nogales, May 10, 1949, 0-0-1.

Fish bait in soil from Juarez, Chihuahua, in passenger's baggage arriving at El Paso, May 21, 1949, 0-3-2.

In soil with two plants in passenger's baggage arriving at Santa Fe bridge, August 13, 1953, 0-0-1.

In soil with plants from Torreon, Coahuila, in passenger's baggage arriving at Santa Fe bridge, August 13, 1953, 0-0-1.

Italy. In soil with strawberry and rosemary plants in baggage on SS Atlantic arriving at New York, March 22, 1950, 0-0-1.

Japan. In 25 lbs. soil with plants in baggage on SS Cavalier arriving at San Pedro, April 23, 1954, 0-0-1.

England. In soil with plants in baggage on SS Britannic arriving at New York, April 17, 1949, 0-1-1.

Wales. In soil with plants in baggage on SS Britannic arriving at New York, April 24, 1949, 0-0-3.

(Worms listed above were intercepted by officers of the Division of Foreign Plant Quarantines, U. S. Department of Agriculture and were available through courtesy of Dr. C. W. F. Muesebeck and Dr. P. W. Oman.)

Texas (probably), 0-0-3. Ottys Sanders. (In an unlabelled tube along with *B. tumidus*.)

External characteristics. Length, 25-42 mm. Diameter, at clitellum, 2-3 mm. Segments, 101 (1), 102 (1), 104 (1), 109 (2). Pigmentation, whenever recognizable (formalin preservation), red. Body rather four-sided posteriorly. Prostomium epilobous, tongue open. Nephropores (when recognizable) just above *B* or above *D*. First dorsal pore at 5/6.

Female and male pores equatorial. Male pore tumescences confined to xv or extending well into xiv and xvi (10).

Clitellum saddle-shaped, on (xxiii?) xxiv-xxx (1), (xxiii?) xxiv-xxxi (2), (xxiii?) xxiv-xxxii (2), xxiv-xxx (2), xxiv-xxxii (1), xxiv/2-xxxii/2 (3), xxv-xxxi (9). Tubercula pubertatis lacking or possibly represented by quite indistinct areas on xxvi-xxx (several).

Internal anatomy. Calciferous gland, intestinal origin, gizzard and typhlosole as in *tumidus*. The typhlosole has no ventral groove anteriorly and, in a worm of 109 segments, ends in xcvi. Hearts were recognizable only in vii-xi (1) or viii-xi.

Seminal vesicles quite small. Atrial glands markedly protuberant into coelom. No setal follicles especially protuberant from parietes (genital setae lacking?).

Life history. Spermatozoal iridescence was not recognized on male funnels and spermatophores were lacking externally though the clitellum in some of the worms appeared to be at maximal tumescence. Parthenogenesis and male sterility are suspected.

Abnormality and *variation.* Helicometameres were noted behind clitellar region in two worms. Seminal vesicles were lacking in ix but were present in x of two worms.

Remarks. Many worms lacked the posterior end and most were poorly preserved. If pigment once was present in alcoholic

material it had become unrecognizable. Anterior and posterior margins of clitellum, as in *tumidus*, occasionally may not be distinct because of quite gradual decrease in height of epidermis. Whether male deferent ducts are looped on posterior faces of funnel septa was not determinable.

If the usual assumption as to American origin of *B. parvus* is correct, this species is the only American lumbricid that has become "peregrine". It had been recorded, usually without data as to variation, from at least sixteen states, as well as from Mexico, Guatemala, Brazil, Hawaii, Japan, Manchuria, China, Tibet, India, Burma, the Malay Peninsula, Java, Germany and the British Isles.

Two species recognized by Smith (1917), *B. parvus* and *beddardi*, were distinguished from each other almost only by differences in clitellar location and in intersetal spacings that now appear to be within limits of normal intraspecific variation.

B. parvus is distinguishable from *tumidus*, also with about 40 partitions or chambers in the calciferous gland, only by clitellar characteristics. The organ tends to be shorter, usually of 7-8 segments, though 9 have been found and 10 may be possible. Situation of anterior margin at 23/24 or 24/25, even at 22/23 when anterior margin is less definite, provides a further distinction but not, in the latter case, from *longicinctus*. To that species one such specimen, with a clitellum also covering xxxi-xxxii, would have been referred but for its foreign origin.

So much emphasis on the clitellum is required because of more or less recent elimination in *Bimastos* of spermathecae, tubercula pubertatis, perhaps also genital setae and certain glands. Species usually differ most obviously from one another, in the Lumbricidae as well as other earthworm families, in their reproductive organs on which the classical taxonomy largely has been based. Satisfactory substitutes for the characters that are no longer available still have to be found, not only in the Lumbricidae but also in other genera where similar evolutionary changes have been or still are under way (cf. Gates, 1954, p. 237).

ADDENDUM

Eisenia rosea (Savigny, 1826)

External characteristics, of several American alcoholic specimens, are such as to permit identification as *B. parvus*. Just as in that species, seminal vesicles of ix-x and all spermathecae are lacking. However, enlarged setal follicles are protuberant, in each worm, into coelomic cavities of one or more segments; *a-b* or *c-d*/x-xiii, *a-b*/xxv, xxxii. Such follicles, with genital setae, are to be expected in those very segments in the exotic *rosea* where their presence usually is indicated by genital tumescences, but apparently not in any American species of *Bimastos*.

The calciferous glands of *rosea* were described by Smith (1924) immediately after those of *parvus*. The only difference mentioned is in width of lamellae and of chambers.

Tubercula pubertatis have been lost during evolution of an A morph ("*Bimastos* stage") in species of several lumbricid genera, and their absence in these athecal individuals of *rosea* is not, then, surprising.

Follicles that are to produce genital setae become enlarged, in this as well as other exotic species, during a juvenile stage before development of tubercula and clitellum which appear ontogenetically in that order. Tumescences develop around apertures of GS follicles as the clitellum is differentiated. Suppression of GS tumescences in this American parthenogenetic strain may be an early stage in an evolutionary development that will result in elimination of the associated GS follicles and their modified setae. Just such an early stage apparently has been reached by certain species of *Bimastos*. In others, *tumidus* and *parvus*, such evolutionary development may have been completed. Genital setae, presumably functioning only during copulation, are of no use to animals that have become parthenogenetic.

V

Bimastos palustris Moore 1895

New Jersey, 0-0-7. Harold Davies (1954).

External characteristics. Length, 18-38 mm. Diameter, 1 mm. or slightly more at posterior end, *ca.* 2 mm. anteriorly, 2+ mm. in clitellum, 3 mm. in xv-xvi. Segments, to 101 (cf. Table 2).

Pigmentation red, in circular musculature of dorsum anteriorly, lacking close to intersegmental furrows but present in ventrum of first five or six segments, recognizable only after stripping off longitudinal musculature, a light pink coloration all that is visible externally. Body squarish posteriorly and with setae at corners. Prostomial tongue broad, short, open (7). Setae begin on ii on which all are present (7), $AB=$, $<$ or $>$ CD, but difference slight, $BC < AA < DD < \frac{1}{2}C$. Nephropores certainly recognizable only behind xv, irregularly and asymmetrically alternate between levels just above B and dorsal to D. First dorsal pore on 5/6 (6), ?6/7 (1), a weak spot at mD on 4/5 in one worm clearly not a definite pore.

Female pores diagonal to transverse slits (or in such slits?), posterolateral to b (7), at most midway between eq/xv and 15/16. Male pores deeply invaginate, the usual transverse cleft apparently slightly postequatorial in some but probably really equatorial on all. Male pore tumescences conspicuous, maximal height at or close to 16/17, sloping anteriorly down to the cleft, scarcely noticeable anterior to eq/xv.

Clitellum annular (7), epidermis not as thick in AA as dorsally but intersegmental furrows unrecognizable (6), anterior and posterior margins distinct and as much so ventrally as in the dorsum (7), on xxiii-xxvii (1), xxiii-xxviii (6). No tubercula pubertatis (7).

Genital tumescences include a-b setae, on xiii (7) and xvi (7).

Internal anatomy. Septa back to 14/15 somewhat more opaque than posteriorly, 8/9 apparently the thickest, 7/8-9/10 less so, all weak — merely pushing gut over to one side or the other breaks the septa at parietal insertions, even anteriorly. Pigment apparently lacking in longitudinal muscle band at mD and in peritoneum.

Calciferous gland extends into x (7), the gut in that segment with an appearance as of two vertical sacs posteriorly. Constrictions at 10/11-11/12 usually slight or unrecognizable but in one specimen so deep externally that the gland appears to be moniliform as in *Eisenia lönnbergi* (Michaelsen, 1894) and *E. carolinensis* Michaelsen 1910. Constriction at or near 12/13 external or internal or both and then different on opposite sides. Intestinal origin in xv (7). Gizzard in xvii-xviii (7). Typhlosole begins rather gradually behind the gizzard and is a simple lamella,

slightly thicker ventrally, often reaching floor of gut, ending as shown in Table 2.

Subneural trunk mostly unrecognizable but occasionally indicated, on ventral face of cord, in two worms by an indistinct red streak visible only in a segment or two. Extra-oesophageals, presumably empty, unrecognizable. Hearts in vii-xi (7), those of vii empty and small (4), all empty (1). A vertical red column, resembling a blood vessel and doubtless of blood, recognizable in lateral wall of calciferous gland on each side in one or more or all of x-xii. Nephridial ducts, at least behind xv, pass into parietes at *B.*

TABLE 2

Typhlosole termination and segment number in *Bimastos palustris* and *B.* sp.

Typhlosole ends in segment	Atyphlosolate segments	Number of segments	Remarks
47	8	55	Posterior amputee
48	4	52	Posterior amputee
62	6	68	Posterior amputee
69	8	77	Posterior amputee
83	10	93	Posterior amputee?
84	11	95	Posterior amputee?
87	14	101	
		B. sp.	
101+?	?	101	Posterior portion broken off and lacking.
130	17	147	

Seminal vesicles equisized and fairly large, in xi-xii (7). Male funnels large, crenellate, reaching well up at sides of gut. Male deferent ducts straight, those of a side coming into contact in xii, passing up to apex of atrium where primary male pore doubtless is located. Spermathecae lacking, rudiments unrecognizable in parietes after removal of longitudinal musculature (7). Ovisacs present (7), lobed, smaller than the ovaries. Ovi-

ducts seem to be unusually thick relative to size of worm and obviously pass into parietes behind eq/xiv.

Atrium thumb-shaped, erect in xv, reaching well up toward level of dorsal face of gut (7), basal portion distended posteriorly and continued into xvi as a transversely placed reniform mass that bulges back 16/17 at parietes. No corresponding extension on parietes anteriorly.

Follicles of ventral setae of xiii and xvi slightly thickened but thin-walled, elongated, apices reaching into coelomic cavities just above associated glands. Acinous glandular masses on parietes median and posterior to each such pair of follicles.

Abnormality. Male pore of right side and atrium in xvi, right male tumescence in xvi-xvii. Basal gland of atrium in xvii. Genital tumescences of right side in xiii and xvii. Clitellum not as thick ventrally in *BB* as in other worms and intersegmental furrows faintly indicated across mV.

Habitats. Apparently restricted to banks that are kept moist by running water (cf. Moore, 1895 and Davies, 1954).

Natural history. Slight iridescence is recognizable on male funnels of two specimens with spermatophores, but not on funnels of other worms.

Spermatophores were found by Moore from latter part of February to December. Cocoons may then be deposited in any season of the year that temperature permits. Although not now anticipated in the summer, some sort of a diapause may be expected in January or whenever the weather is too cold for normal activity.

Biparental reproduction can be assumed, at present, as Moore mentioned release from spermatophores of sperm presumably normal.

Distribution. Pennsylvania, within thirty miles of Philadelphia. Northern New Jersey. Raleigh, North Carolina. The latter record was accompanied by no information as to habitat, number of specimens, structure, etc.

Remarks. Greater opacity of epidermis than usual in the dorsum anteriorly, *in vivo* as well as after preservation, presumably is responsible for a previous assumption as to absence of pigment (cf. Smith, 1917, p. 169).

Spermatophores are 2-2+ mm. long, attached to xiv in *DD*.

Male pore tumescences in the types, so far as can be judged

from the figure provided by Moore, seem to have been as marked anterior to the cleft as behind it.

The calciferous gland appears to be constricted at or near insertion of 12/13 as in various other American lumbricids both exotic and endemic. The constriction may be external on one side and internal on the other or internal all around when gut is straight. These differences probably are of little significance, perhaps a matter of differential contraction at time of preservation. However, the constriction is usual and in dissections appears to provide a posterior boundary of the gland though calciferous lamellae, according to Smith (1924) frequently extend into xiii.

Hearts did not pass in any of these specimens into gut wall (cf. Moore, 1895) which confirms Smith's finding (1928, p. 354). The vertical cords of blood mentioned above may have been mistaken for hearts. Inability to trace the extra-oesophageal trunks in the present specimens is unfortunate because of a possibility that they may provide characters of taxonomic importance in a group where such are much needed. However, it can be suggested, after examination of the vessels in many specimens of various other species that the extra-oesophageal trunks do not join the ventral trunk in x (Moore, 1895) or the dorsal trunk in x (Smith, 1928). Distention by blood of an anterior portion of the extra-oesophageal and of a fairly large branch that occasionally passes (in other species) to the dorsal trunk in ix and/or x, with the portion of the extra-oesophageal behind the branch empty and collapsed, may have been the condition seen by Smith. A branch from the subneural arising in any of segments xiv-x (again in other species) may pass to the extra-oesophageal. When that branch is distended with blood the trunk at first appears to turn laterally and join the extra-oesophageal but does again become recognizable anteriorly wherever blood is present. The difficulties posed by temporarily empty vessels in earthworms rarely have been appreciated even by those who made special studies of the circulatory systems.

Microscopic examination of the setae in the enlarged ventral follicles of xiii and xvi has not been possible. Some modification certainly can be expected even though not recognized by Moore nor mentioned by Smith.

B. palustris is distinguished from the previously erected species, *tumidus* and *parvus*, by the shorter elitellum of only 5-6 segments as well as its obvious annularity, posterior dislocation of female pores, deep invagination into coelom of male pores at apices of large atria, the enlarged setal follicles in xiii and xvi, the epidermal tumescences and the coelomic glands ("postsetal", Moore) associated with those follicles. The follicles, genital setae therein, glands and tumescences have not been used in the classical taxonomy. Little is known, however, about the variation of any of these characters in this species or of the newer ones just mentioned in any lumbricid. Another distinction from *tumidus* and *parvus* may be in the method of reproduction.

Closest to *palustris* of the *Bimastos* species now appears to be *heimburgeri* Smith 1928, erected on a single specimen from Illinois. Four individuals subsequently recorded from North Carolina, in absence of any description, must be assumed to be like the type. The species is distinguished from *palustris* by the clitellum, of 8+ segments on xxv-xxxiii(part) and saddle-shaped, absence of genital setae and presumably also of the acinous glands. The type was not "sexual" though clitellate, and Smith suggested (1924, p. 356) that genital setae "may be present at the time of sexual activity." This now seems unlikely. Enlargement and protuberance into coelom of GS follicles is obvious in lumbricids studied by the author before any indication of clitellar development is recognizable, and in thecal species even before appearance of the tubercula pubertatis. If Smith's statement *re* gonads of diminished size referred to the testes, and if clitellar tumescence was maximal, the type may be parthenogenetic. Otherwise iridescence should have been recognizable on the male funnels of the unsectioned half and in the sections of the other half sperm on the funnels should have been obvious.

Bimastos sp.

Moonshine Dell, Giles County, Virginia, June 20, 1955, 0-0-2. Prof. Walter Harman.

External characteristics. Size, 74 x 4.5 (at xv) mm. Segments, 147. Pigmentation red, in dorsum but sparse behind elitellum until near hind end, in ventrum of first seven seg-

ments. Body approximating to transversely rectangular in cross section posteriorly, with setae at the corners. Setae begin on ii on which all are present, rather closely paired, AB *ca.* $= CD$, BC *ca.* $= AA$, $DD < \frac{1}{2}C$ posteriorly. Prostomium epilobous, tongue open (2 specimens). First dorsal pore on 5/6 (2). Nephropores unrecognizable.

Clitellum annular, only slightly tumescent, intersegmental furrows recognizable all around, on xxiii-xxxi (1), still quite indistinct on the other but apparently indicated by a whitening of the dorsum on xxv-xxx. Tubercula pubertatis lacking.

Female pores definitely equatorial on xiv, of about the same size and shape as adjacent aperture of a GS follicle. Male pores each in a deep equatorial cleft or slit at bottom of a depression sloping down from 15/16 and 14/15, tumescences markedly protuberant, extending across all or nearly all of xiv and xvi, equally developed anterior and posterior to eq/xv.

Genital tumescences unrecognizable (perhaps not yet developed) but *a-b* setae of xii-xviii retracted into parietes, follicle apertures enlarged, slit- or comma-shaped, longitudinally placed.

Internal anatomy. Septa 8/9-14/15 strengthened, 12/13 the thickest. Pigment sparse in longitudinal musele band at mD. Peritoneal flecks very few.

The calciferous gland extends well into x and there is widened so that there is an appearance as of two vertical sacs. A slight constriction at insertion of 10/11, none at 11/12, internal at 12/13. Intestinal origin in xv (2). Gizzard in xvii-xviii (2). Typhlosole begins in xxii, nearly 2 mm. high but rather thin anteriorly where it reaches floor of gut, and has a deep longitudinal groove on ventral face, ending abruptly (cf. Table 2).

Subneural trunk recognizable only for a distance of one segment here and there where a little blood is present. Extra-oesophageals empty but traceable (1) into dorsal trunk posteriorly in xii. Hearts present in vii-xi, empty in vii (1) or with a little blood but small. Nephridial ducts pass into parietes at *B*.

Seminal vesicles rather small, tough, in xi-xii. Male funnels crenellate. Male deferent ducts without looping on funnel septa. Ovaries and ovisacs as usual, spermathecae absent (2).

Atrium hemispheroidal, the lumen reaching above level of parietes, with glandular extensions into xvi and xiv. Follicles of ventral setae of xii-xviii enlarged and conspicuously pro-

tuberant above parietes. Acinous glands apparently are associated with the follicles.

Remarks. Thickened septa, nephridia, GS follicles and acinous glands are closely crowded and adherent to each other. Determination of relationships in such circumstances sometimes becomes possible after several months further treatment with preservative.

Enlarged apertures of GS follicles presumably are common external openings of the follicles and of the associated acinous glands.

Atria are not as high as in *palustris*.

Spermatozoal iridescence on male funnels is slight. Such iridescence has been noted in other lumbricid species during postsexual regression, at onset of maturity, and when maturation is sparse as in certain supposedly parthenogenetic forms.

These worms are to be compared with those of species having the anterior margin of the clitellum at 22/23, *palustris*, *longicinctus* and *parvus* (only occasionally). They cannot go in *palustris* as at present understood though they do have GS follicles in xiii and xvi and acinous glands associated therewith. Presence of those follicles and glands presumably rules out *parvus* in which they are lacking. Nothing is known as to GS follicles and glands in *longicinctus* in which the clitellum is saddle-shaped though this latter difference may prove to be of no importance.

Bimastos sp.

Whitetop Mountain, Virginia, under bark of log at elevation of 4700 feet, August 17, 1955, 0-0-1. Prof. Walter Harman.

External characteristics. Size, 16 x 2 mm. (through clitellum). Segments, 61 (probable posterior amputee). Pigmentation red, obvious externally. First dorsal pore at 5/6.

Female pores on xiv, further from *B* than usual, almost at level of male pore cleft, only slightly if at all postequatorial. Male pore clefts equatorial on xv. Male tumescences extend well into xvi and xiv, 14/15 and 15/16 unrecognizable across them, and include *a-b* of xv-xvi. Clitellum annular, on xxiv-xxxii(xxxiii?), posterior margin indistinct. No tubercula.

Internal anatomy. As in previous species except as otherwise mentioned.

Typhlosole ends in liii but is much lower there than in the preceding segment.

Male deferent ducts looped between funnel septa and parietes but in a loosely zigzagged manner, not compacted into a ball or disc. Oviducts pass into parietes anterior to equator of xiv and are relatively thick. GS follicles, *a-b* of xv-xvi, markedly protuberant into coelomic cavities. No acinous glands associated with those follicles.

No atria; even atrial glands lacking.

Parasites. Five transparent cysts, each of about the same size as the prostomium, are present in coelomic cavities of xi-xii.

Remarks. No irideseence recognizable on male funnels.

Species with the anterior margin of the elitellum at 23/24 are *longicinctus* and *parvus.* Presence of GS follicles in xv-xvi (that are lacking in *parvus*) apparently obviates further consideration of that species. Nothing is known as to presence or absence of atrial glands in *longicinctus.*

VI.

Species of Eisenia

The distinctness and relationships of our endemic species of *Eisenia,* which were characterized about as well as their European congeners, have been misunderstood abroad. So little has been known about variation in and distribution of the American forms that the collections made by Dr. Pickford and Prof. Harman, in the hitherto uninvestigated mountains of North Carolina, Tennessee and Virginia (Gates, 1955), though secured in a probably unfavorable season, have proved to be of considerable importance. Material received since completion of the manuscript of parts I-II of this series now has provided some of the additional information that was wanted for a discussion of these relationships.

E. hortensis obviously is exotic in North America. A brief description is included to provide hitherto unrecorded but now necessary information. Notes on other exotics, *E. foetida* and *rosea,* are provided for similar reasons.

The author's thanks are extended to Prof. Walter Harman, Harold Davies, and Curator Fenner Chace, Jr., for the opportunity of studying the various specimens they supplied.

Genus Eisenia Malm 1877

Eisenia carolinensis Michaelsen 1910

Whitetop Mountain, Virginia, August 17, 1955. Under rocks at summit, 4-0-4. Under bark of log at elevation of 4700 feet, 0-0-1. Prof. W. A. Harman.

Mountain Lake, Virginia. Barn, Mountain Lake Hotel, June 20, 1955, 0-0-1. Moonshine Dell, June 20, 1955, 0-0-2. Castle Rock, July 8, 1955, 0-0-1. Prof. W. A. Harman. Mann's Bog, MLBS., August 4, 1955, 0-0-2. Doris Hatfield per Prof. W. A. Harman.

Segments, 133 (2 helicometameres in intestinal region), 136, 141, 144 (all juvenile), 141 (largest clitellate worm, 110 x 7 mm), 152. Pigmentation red, quite dense in juveniles and obvious externally clear to hind end, also externally recognizable all the way to the anal region in one clitellate worm but in others visible just in the preclitellar portion of the body and even there sometimes indicated only by a faint pink. Pigment appears to be sparse in dorsum of ix-xii, except near mD, of the clitellate worm with most obvious red color. Clitellum whitish or light grayish and, even though in formalin, about as in previous alcoholic material.

Tubercula pubertatis as before, quite rudimentary but obviously tripartite on two late juveniles. Variation in location of genital tumescences and clitellum is shown in the table.

The typhlosole ends in cv, but is smaller in last two or three segments (worm of 141 segments), cxiv (152 segments).

Seminal vesicles of a juvenile are large, filling coelomic cavities except in ix, very soft and fragmenting on slight pressure even after a month in formalin (preservation very good). Testes discoidal. Iridescence lacking on male funnels.

Remarks. The red coloration in clitellar epidermis previously mentioned (Gates 1955, p. 8) must have been slowly developed in the formalin. No trace of the coloration is as yet recognizable on these recently preserved worms.

TABLE 3

Variation in external characteristics of *E. carolinensis* from Virginia

Serial number	Genital tumescences, including *a-b*, additional to those on xxv-xxx, located in segments	Clitellum on segments	Remarks
1	11 17 18 31		Juvenile. TP rud.
2	11 17 18 31	24-32/eq	
3	11 17 21 24 31	24-31	
4	11 18 21 31	24 32	Sph.
5	16 17	eq/24 31	
6	16 17 21 31	(23?)24-31	
7	16 17 21 31	24-31	
8	16 17 21 31	24-31	
9	17 21 31		Juvenile. TP rud.
10	17? 24 31		Juvenile.
11	17 21 31	24-31	
12	17 21 31	25-31	
13	17 18 20 21 31	24 32/eq	
14	17 24 31		Juvenile.
15	21 31	25 31	

TP rud. Tubercula pubertatis rudimentary. (Rudiments still unrecognizable in other two juveniles.)

eq Equator.

Sph Small spermatophore median to *A* on right side of xxvii.

Genital tumescences on juveniles are, of course, still rudimentary but are definite except at the one site indicated by a "?".

Two small knobs mark sites of invisible follicle apertures on each of the conspicuous tumescences of clitellate worms.

EISENIA LÖNNBERGI (Michaelsen, 1894)

Pigment, in or associated with circular muscle layer, obviously is not red and that layer, after stripping off the longitudinal musculature, has a dirty or sooty appearance somewhat suggestive of an India-ink suspension. Externally, pigment appears to be lacking in the dorsum of viii-xii except close to mD, but after removal of longitudinal musculature is recognizable though more sparse than elsewhere. Peritoneal flecks appear to be black and they may be numerous and large.

Clitellum greyish (formalin preservation), on xxiii-xxx (2), xxiv-xxx (1). Genital tumescences, including *a-b*, on xii (1), xxiii-xxx (2), xxiv-xxx (1).

Typhlosole ends in xci (worm of 108 segments and like the other two a posterior amputee).

Hearts of x-xi empty and slender (3). From the subneural a large branch passes up on anterior face of 13/14, on each side, to dorsal trunk. Extra-oesophageals again empty, traceable only in one worm and then just into xii.

Male deferent ducts may be quite obviously looped just behind funnel septa but loops are loose, not bound by connective tissue into a disc or ball. GS follicles of xii surrounded on parietes by annular glands. Glandular tissue is median to *A* on parietes in xxiii or xxiv to xxx but is lateral to *B* only in xxvi-xxix (and there TP glands?). GS follicles of xxiii or xxiv to xxx (as well as of xii, in 1 specimen) conspicuously protuberant into coelom, those of xxvi-xxviii somewhat more so.

Remarks. These New Jersey worms (Davies, 1954, p. 6) had not been in formalin long enough to permit development in clitellum of the red coloration previously mentioned (Gates 1955, p. 2). The dark coloration previously mentioned (*ibid.*, p. 6), that often "develops" during preservation when formalin is in contact with cork, obviously is not involved here.

Gut lumen in xi-xii may be only a vertical slit as shown by Smith (1924, figs. 25, 28) or the lumen may be much larger, even wider than the gut wall. Differences presumably are due to physiological state of glands at time of fixation and/or to variation in method of preservation. Even with greatest width of lumen and maximum narrowness of the wall the calciferous gland is obviously moniliform. The gland always appears, in horizontal sections, to end without reaching into segment x.

Relationships of glandular masses on parietes in clitellar region still remain to be determined; distinguishing setal glands, possible peritoneal blisters elevated by accumulations of some kind of corpuscles, and compacted masses of coelomic coagulum, from each other and from possible TP glands not permitted by material that has been available. If TP glands are lacking, *lönnbergi* will have one more character in common with *carolinensis* as well as *E. foetida* (Savigny, 1826). Presence of TP glands will be shared with *hortensis*.

Eisenia foetida (Savigny, 1826)

External characteristics. Spermathecal pores appear to be slightly more lateral to mD than in American species. Male pores each at lateral end of a slight cleft and at or slightly lateral to m*BC*. Tumescences slight, restricted to xv and to median half of *BC*.

Clitellum of 6-8 segments, usually beginning at 24/25 or 25/26 and ending at 31/32 or 32/33. Tubercula pubertatis extending across three or four segments, on xxviii-xxx (most frequently), xxviii-xxxi, or between equators of those segments.

Genital tumescences often quite distinct, in the clitellar region as obvious as in the macedonian form of *E. rosea* or indicated only by deep retraction of genital setae, each tumescence around a setal couple. Any pair of ix-xii or each couple of one of those segments may be involved but there is considerable variation as well as asymmetry. Ventral couples of xxvi-xxxii usually are included in tumescences, those of xxv, xxiv and xxxiii less often, in one of xvii-xxiii much more rarely.

Internal anatomy. No septa thickly muscular. Calciferous gland begins behind insertion of 10/11, much wider in xii, with a slight external constriction at 11/12 and an internal constriction at or just behind 12/13 on one or both sides. No trace of sacs in x. Gizzard variable, layer with brilliant muscular sheen in horizontal section ends at or slightly behind insertion of 17/18 or is continued though with decreasing thickness to or nearly to 18/19. Gut narrowed in xix and valvular at 19/20.

Dorsal blood vessel empty and unrecognizable anterior to 5/6. Subneural trunk adherent to cord. Extra-oesophageals turn up in ix, pass through 9/10 and into dorsal trunk on posterior face of 9/10, a posterior continuation of the trunks behind the upward bend recognizable in none of the specimens. Hearts in vii-xi only (20), no branches from dorsal trunk in vi (20), hearts of x-xi usually smaller than those of ix. Nephridia appear to be vesiculate, shape of bladder doubtful (J-shaped?). The duct, very short and slender, passes into parietes at *B*. Necks of funnels sometimes are long enough to reach into contact with septum next in front (contracted material). Brain and circumpharyngeal commissures left in iii by a transverse section exactly along 3/4.

Holandric. Seminal vesicles, four pairs, in ix-xii (20), one vesicle of xii occasionally extending into xiii and markedly constricted by 12/13. Male deferent ducts rather thick entally, just behind funnel septa irregularly and variously looped, connective tissue binding loops together delicate and easily ruptured, the looped portion ("epididymis") sometimes reaching a length of 2 mm. Ovaries, ovisacs and oviducts as usual, except that an extra ovary (with large ova distally) is present though not associated with a female funnel or ovisac in two of ten Maine worms. Spermathecae free, in ix-x (20), a short duct portion often recognizable in coelom.

Atrial and TP glands lacking (20). GS follicles (those in tumescences) protuberant into coelom but often bent laterally (*a-b*) or mesially (*c-d*) against parietes. The "postsetal glands" unrecognizable (field preservation) but some slight parietal blistering around GS follicles usually is recognizable.

A half-moon-shaped slight elevation with base at *D* extends on parietes in viii or ix-xii, well toward mD and coincides with an obvious external white area in which the epidermis is thickened. The parietal elevation appears to be little more than an accumulation of flocculent matter (corpuscles?) underneath elevated peritoneum. Protuberance, like the epidermal thickening, is most marked when pigment associated with circular muscle layer has been completely lysed, less marked when lysis is as yet only partial.

Reproduction. Male funnels, in a large number of clitellate worms, always have a brilliant spermatozoal iridescence. A similar iridescence usually is recognizable in spermathecal ampullae. Spermatophores often are present externally. Reproduction presumably is sexual and probably almost always biparental.

Remarks. The above characterization, based on material from ten states, supplements a previous description (Gates, 1943, p. 95) published after side by side comparison of "wild" worms and those being sold by earthworm culturists as "hybrids."

Nephropores, as before, could not be identified with certainty though possible sites on some segments may be slightly more lateral to *B* than usual.

Eisenia hortensis (Michaelsen, 1890)

Urbana, Illinois, April 25, 1923, 0-0-3. J. L. Hyatt per F. Smith (U. S. Nat. Mus. No. 26205).

External characteristics. Segments, 85-103. Pigment unrecognizable externally (alcoholic preservation). Prostomium epilobous (3), tongue open. Setae begin on ii, on which all are present, paired, *AB ca.*=*CD* apparently < *BC*, *d* rank about at mL anteriorly, somewhat more dorsal posteriorly where *c* rank seems to be at mL. Nephropores small, first recognizable on iii, located on left side of one specimen as follows: iii-iv/*D*, v/well above *D*, vi/nearer mD than to *D*, vii-ix/*D*, x-xi/slightly above *B*, xii-xiii/*D*, xiv-xvi/above *B*, xvii-xviii/*D*, xix-xx/above *B*, xxi-xxii *D*, xxiii/above *B*, xxiv/*D*. Both pores of xiv are just above *B* (1) or at *D* (2), both pores of xv-xvi just above *B* (3). First dorsal pore at 5/6 (3).

Spermathecal pores minute, each on a tiny tumescence close to mD, on 9/10-10/11. Female pores minute, just above *B*, equatorial on xiv. Male pores minute, about the same size as nephropores and smaller than the female pores, each laterally in a slight equatorial cleft (almost unrecognizable in one worm with greatest protuberance of tumescences), on xv in median half of *BC*. Tumescences markedly conspicuous, confined to median half of *BC*, longitudinally elliptical, bulging 14/15 anteriorly and interrupting 15/16 to reach well into xvi.

Clitellum saddle-shaped, unrecognizable below *B*, on xxviii-xxxii (2), xxviii-xxxiii (1). Tubercula pubertatis on xxx-xxxi at least, apparently reaching onto xxix and to xxxii/eq (2), longitudinal bands of translucence without any indication of elevation (2), each band on median face of a markedly protuberant and rather lamelliform ridge highest on xxx-xxxi and gradually disappearing on xxix and xxxii (1).

Genital tumescences indistinct, setae retracted out of sight, *a-b*/x (1), *a-b* and *c-d*/x (1), *c-d*/xi (1). Unrecognizable posteriorly.

Internal anatomy. Septa, none thickly muscular. Pigmentation still unrecognizable after stripping off longitudinal musculature but circular layer not white as is the other.

Gut wide in x, with wall thin to 10/11, no trace of sacs. Calciferous gland in xi-xiii, not quite reaching 10/11, no special

constrictions recognized. Intestinal origin in xv (3). Gizzard in xvii (3), the layer with brilliant muscular sheen obviously extending in horizontal sections only slightly behind 17/18. Gut narrowed and valvular at 19/20 (3). Typhlosole begins in region of xxi-xxiii and is simply lamelliform, ending in lxxvi (worm with 85 segments), lxxxix (100 segments), xc (103 segments).

Dorsal blood vessel recognizable into v, with two pairs of vessels to gut in each segment from xii posteriorly, one pair anteriorly in each of xi-x, none in ix. Extra-oesophageals and subneural trunk unrecognizable. Hearts in vii-xi (3). Nephridia vesiculate, the vesicle usually collapsed but when distended elongately ellipsoidal and extending on the parietes from *A* or *B* to beyond *D* or almost halfway to mD. Ducts not certainly recognizable, probably very short and passing into parietes at *B*. Brain and circumpharyngeal commissures left in iii, once well anteriorly, by a transverse section exactly along 3/4. Pharynx roof in iv with a median groove that shortly divides so that lumen is Y-shaped in transverse section.

Testes in x-xi (3), male funnels medium-sized and crenellate. Male deferent ducts straight, without sinuosities or looping (no epididymis), uniting posteriorly in xii, passing posteriorly about at m*BC* and into anterior margin of atrial gland laterally. Seminal vesicles in ix, xi and xii, those in ix the smallest. Ovaries, ovisacs, oviducts as usual. Spermathecae in ix-x (3), ducts practically confined to parietes.

Atrial glands low, finely acinous, tough, longer than wide, in median half of *BC*, apparently reaching into xvi. TP glands on each side, a longitudinal tough mass with an acinous appearance like that of the atrial gland, in xxx-xxxi, possibly extending slightly into xxix and xxxii, in the worm with ridges almost concealed from view in a deep groove.

GS follicles not especially thickened but protuberant above general level of parietes, anteriorly as indicated by the tumescences, posteriorly *b* of xxx-xxxi (3), xxix (2), xxxii (1). The *a* follicles of xxix-xxxii appear to be slightly enlarged and slightly protuberant into coelom.

Reproduction. Two spermatophores present in *AB* in presetal half of xxviii (1) have an opaque central portion with slight iridescence. Spermatozoal irideseence on male funnels and in

distended spermathecae brilliant. Biparental reproduction is anticipated.

Remarks. These worms had been preserved in near-maximal relaxation and guts are only partially filled. They are too soft, though not macerated, for convenient study of external characteristics. Inability to recognize genital tumescences posteriorly probably results in part from the method of preservation. Nephropores, however, in several regions are visible under high power of dissecting binocular as definite openings. Blood in distended hearts is perfectly white and this bleaching is of no assistance while looking for the subneural trunk or in learning relationships of the extra-oesophageals. Blister-like parietal elevations, around *a* and *b* setae of xvi (with slight indications of lobing), and extending uninterruptedly through clitellar segments exactly in *AB*, may be artifacts (?).

The clitellum of the only other specimen seen (Gates, 1943, p. 96) was on xxvii-xxxiii. More anterior extension, across xxv or even xxiv-xxv, apparently indicated by Smith (1917, p. 166), may have been lacking in his own material.

Asymmetry in intrasegmental location of nephropores was recognized or suspected only very rarely and may be less frequent than in some species though condition of material did not permit enough observations for a more definite characterization.

Anterior termination of calciferous gland behind insertion of 10/11 in *hortensis*, previously recorded by Smith (1924), certainly appears to be more than sufficient justification for specific distinction from worms in which the gland extends well into x.

The taxon *hortensis*, originally a forma of *Allolobophora subrubicunda*, eventually became a variety of *veneta* in *Eisenia*, then a species in *Eisenia* (Omodeo, 1952, p. 188), and lastly a species in *Dendrobaena* (Omodeo, 1955, p. 6). The transfer to *Dendrobaena*, along with *veneta*, seems unlikely to assist in resolving any of the confusion so prevalent in lumbricid taxonomy.

Variation greater than usual in a species seems to have been imputed to *hortensis*, which may be in need of revision and more accurate definition. The species will have to be considered as characterized above, in the discussion (p. 29), since European material has been unavailable and examination of the types has been impossible.

Eisenia rosea (Savigny, 1826)

This species is polymorphic, various formae that have been named being distinguished almost entirely by differences in the reproductive system. Number of chromosomes already recorded (cf. Muldal, Omodeo); 54 = 3n, 72 = 4n, 90 = 5n, 108 = 6n, 160 to 174 = 10n-6 to 20. Ploidy varies within the formae. Very common, probably throughout most of North America, possibly more so than any other parthenogenetic species. Most of the material available from a dozen states appears to be referable to forma *macedonica* which has, according to Muldal, 53 chromosomes = 3n-1.

Calciferous glands, as previously noted by Smith (1924, p. 32, fig. 44), extend well into x. No variation with regard to that character was found during examination of a considerable number of specimens. Differences in appearance and size of "saes" as well as of other portions of the gland are recognizable but presumably are expressions of physiological state and/or variety of fixation and preservation. Hearts are present in vi.

Atrial glands are lacking but TP glands are present, except in more advanced stages of morph evolution in which spermathecae and some of the seminal vesicles also may be absent.

Transfer of *rosea* to *Allobophora*, proposed by Pop (1941) and approved by Omodeo (1955), may prove to be no more acceptable than retention in *Eisenia* where the species may as well remain, in hope of avoiding frequent changes in name of a widely distributed worm, pending the drastic revision of the entire family Lumbricidae that is so much needed.

DISCUSSION

The close relationship of the American species of *Eisenia* to each other is shown by many characters to which little or no attention has been given in the past. Among such are: segment number, maxima — so far as known at present — being 142 in *lönnbergi,* 152 in *carolinensis;* lysis of pigment, at maturity, in dorsum of viii or ix-xii; alternation of nephropores between two widely separated levels and the frequency of intrasegmental asymmetry in position; size and shape of the typhlosole as well as its length, termination being anterior to cxvi; abortion of hearts or commissures in v but presence of such vessels in vi;

emergence of spermathecae, during their development, into coelomic cavities so far that ducts are not confined to parietes; the large battery of GS follicles which includes the *a-b* setae of xxv-xxx, and frequently of additional segments as well (taxonomic value of characters of genital setae as yet uninvestigated). Close pairing of spermathecal pores near mD, in these species, though perhaps not always in the Lumbricidae, absence of seminal vesicles in x, etc., provide further evidence of close relationship.

Taxonomically important differences between *carolinensis* and *lönnbergi*, respectively, are: pigment, red or black (? certainly not red). First dorsal pore located at 5/6 or 4/5. Spermathecae two or three pairs, with pores on 9/10-10/11 or 8/9-10/11. Clitellum of 7-10 or 7-8 segments, ending at 31/32-32/33 or at 30/31. Tubercula pubertatis, on xxvii-xxix or xxvi-xxviii. An "epididymis" present or lacking. Spermathecae, preseptal or postseptal. GS glands lacking in coelom or present on parietes. Another difference of some importance, if established, will be absence or presence on parietes of TP glands. Male tumescences of xv usually are larger in *carolinensis* but shape, size and segmental extent, which occasionally have been cited as evidence for specific distinctness in closely related forms (Kobayashi, 1940, p. 289), may have little or no such value. Additional differences may be anticipated, perhaps in the genital setae, as sexual setae in other families of earthworms have been thought to have considerable taxonomic value (cf. Pickford, 1937), as well as in other systems as yet unstudied.

Difference in pigmentation of two such closely related species is of especial interest as it demonstrates the futility of attempting to divide the Lumbricidae (Pop, 1941, p. 508), on the basis of that character, into subfamilies. Even generic definition in terms of pigmentation is now impossible, at least in case of *Eisenia*.

Endemicity and distinctness of American species of *Eisenia*, of which there now appears to be only two, have been questioned in several recent contributions ("maldistinte," Omodeo, 1955, p. 50). "In the eastern part of the U. S. A., a few 'endemic' species are found, but," according to Muldal (1952, p. 56), "it seems as if there were no really old species there, and that these

forms are recently introduced and rapidly changed from their European progenitors."

The European species with which relationships first have to be considered are *E. foetida, submontana* and *nordenskiöldi*, none of which has been characterized adequately for present needs. *E. foetida*, the only one available on this continent, accordingly has to be taken as a typical representative of the genus of which it presumably is also the type species.

Close relationships of *foetida* to both American species of *Eisenia* are indeed suggested by many characters, but to *carolinensis* more especially because of pigmentation, number of spermathecae, and location of spermathecal pores. Differences from *carolinensis* include: the shorter clitellum of 6-8 segments; location of anterior boundary of the clitellum at 24/25 or at some more posterior level back to 26/27; location, usually, of tubercula pubertatis on xxviii-xxx or xxxi; abortion of hearts in vi; retention of seminal vesicles in x. Physiological differences may be even more important, for *foetida*, in spite of rather definite restrictions to certain sorts of special habitats, has been able to avail itself of many of the opportunities for colonization in remote areas that have been provided, accidentally or intentionally, by man.

More important, however, and disproving the supposed lack of distinctness, are differences in the calciferous glands. These organs, in *foetida*, according to Smith (1924, p. 28, fig. 20), begin only in xi well behind the insertion on the gut of septum 10/11. No variation in that character has now been found, in many specimens examined for this particular purpose. The glands in the two American species do appear, in dissections (I-II), to be restricted to xi-xii, but microtome sections (Smith, 1924, p. 28, fig. 25) showed that the calciferous lamellae, though gradually narrowed, extend through all of x in *lönnbergi*. The same lack of variation with respect to anterior boundary of the gland, as in *foetida*, can be confidently expected in both American species though the assumption that the boundary is the same in each requires confirmation for *carolinensis*.

Differences just mentioned certainly are of considerable importance and may prove to be of value at subgeneric or even generic level. Resemblances that can justify inclusion of the

three species in the same genus are only: greater thickness of the gland in xii, and absence of any sort of sacs in x.

Presence of calciferous lamellae between 9/10 and 10/11 is tentatively assumed to be primitive, and the anterior narrowing is thought to be evidence that evolutionary reduction of the portion of the gland in x has been under way. Elimination of calciferous lamellae in x has been completed in *foetida*.

The calciferous gland in *hortensis* begins, just as in *foetida*, in xi. That character, together with location near mD of spermathecal pores, abortion of hearts or vascular commissures in v-vi, and other similarities, appear to justify retention of *hortensis* in the same group as *foetida*, unless, of course, presence of atrial and of TP glands in *hortensis* is to be considered of sufficient importance for generic distinction. Such importance at present seems unlikely as those glands sometimes are eliminated, in the Lumbricidae, within infrasubspecific taxa.

The calciferous gland in *E. rosea* not only extends well into x but is there responsible for widening of the gut and for formation of a pair of "sacs." This certainly is adequate justification for exclusion from any genus of which *foetida* is the type.

The calciferous gland in *Dendrobaena octaedra* is, at least in part, moniliform, having a deep external constriction between the portions in xi and xii. This produces a marked resemblance to the glands of *lönnbergi* and *carolinensis*. If sacs are lacking in x, as now appears to be the case, relationships of *octaedra* to other species of *Dendrobaena* must be reconsidered. If the thickening of gut wall in the posterior quarter of x proves to be calciferous, relationships of *octaedra* thereby indicated will be closer to American than to European species of *Eisenia*.

Characters provided by calciferous glands have not been used in lumbricid taxonomy hitherto, except at species level and then, only the number of chambers or partitions in the gland. Such a character now seems unlikely to have much importance as Omodeo (various papers) already has found intraspecific variation that nearly reaches known limits. Other and more readily recognized characters obviously are available. Neglect of, or inadequate attention to, the calciferous glands in the much larger family, the Megascolecidae, was in part at least responsible for the unnatural and morphologically heterogeneous "genera" on which Stephenson (cf. 1930) based his thesis of convergence.

That can be concisely but fairly summarized as a belief that an extant genus evolved, in different parts of the world, from two or more genera all still extant.

Lumbricid genera still are defined (cf. Stephenson, 1930; Cernosvitov and Evans, 1947; Pop, 1941) mostly by genital characters. One such, for example, is number of seminal vesicles, organs that may undergo all of the standard phylogenetic reductions as well as yet others within limits of a single infrasubspecific taxon. All other structures of the same system, excepting only the ovaries of xiii, also are subject to change at species or lower level. In large sections of various earthworm families the genital organs provide most of the macroscopic characters by which species are distinguished and defined. This remarkable evolutionary plasticity (cf. Gates, 1956 b-e) of the reproductive system necessitates considerable caution in use of its structures for taxonomic purposes at genus or higher level.

Pigmentation is one of the four somatic characters and that by which Pop (1941) would subdivide the Lumbricidae. The procedure proposed would place the two closely related American species, as already noted, in different subfamilies. Gizzard characters, at least as usually stated, no longer are diagnostic even for *Eiseniella*. The prostomium may always be tanylobous in *Lumbricus* but the same shape is found occasionally in all but one of the other genera. Setae have provided the fourth character, the value of which is shown by the following quotations from generic definitions (Cernosvitov and Evans, 1947): "Setae more or less closely paired," *Allolobophora;* "closely or widely paired (or distant)," *Bimastos;* "mostly widely paired or distant, rarely closely paired," *Dendrobaena;* "closely to widely paired or distant," *Eisenia;* closely paired (seldom widely paired)," *Eophila;* "(mostly distant) rarely closely paired," *Octolasium*. Such obviously undiagnostic characters, in Pop's system (1941), are second in importance only to pigmentation. Even with more recent changes suggested by Pop and Omodeo, the lumbricid genera appear to be only congeries of species associated because of relatively unimportant or superficial convergences.

As one rather indirect result of a study of evolution of reproductive organ polymorphism (Gates, 1956c) it is now possible to suggest, but only very tentatively because of ignorance of so

much of earthworm anatomy, some of the directions in which evolution may have proceeded in the Lumbricidae, with reference especially to the species that have been considered above.

From a hypothetical protomegadrilid to be characterized elsewhere, an ancestral protolumbricid can be derived by the following changes: Acquisition of dorsal pores at each intersegmental level. Dislocation laterally of spermathecal pores from region of *AB* to *CD*. Differentiation of tubercula pubertatis within the clitellum and in association therewith of coelomic glands (TP) of unknown function. Elimination of any oesophageal gizzard. Extension of oesophagus into xv. Union at median margins of calciferous lamellae of x-xiii or xiv to produce an intramural gland opening anteriorly into gut lumen. Development of an intestinal gizzard in xvii and behind that of a typhlosole. Differentiation of a subneural trunk and, median to the hearts, of extra-oesophageal trunks. Elongation of male deferent ducts to open to exterior in *BC* at equator of xv. Invagination into coelom of xv of atria (with glands thereon) through which male ducts opened to exterior. Slight elongation of oviducts to open at equator of xiv just lateral to *B*. Specialization of setae in anterior segments for genital functions. Other characteristics that can be assumed are: presence of lateral hearts or commissures in v-xi. Penetration of nephridial ducts into parietes to open externally at or near *B*. Presence of glands of unknown function in association with follicles of genital setae, and presence of four pairs of seminal vesicles in ix-xii. The spermathecal battery already had been enlarged by addition of two pairs with pores at 9/10-10/11, or shortly was so augmented.

A more recent ancestor of most species hitherto included in *Eisenia* had continued dislocation of spermathecal pores toward mD and regardless of positions of setae, begun reduction of calciferous lamellae of segment x, aborted hearts or commissures of v, acquired a tendency for nephridial ducts during embryonic development and, after parietal penetration, to grow laterally before passing on to the epidermis, eliminated the original pair of spermathecae that had opened at 8/9, aborted atria and even the atrial glands. If that ancestor had a clitellum of six or seven segments with anterior margin at 23/24 little change additional to acquisition of the peculiar dark pigment, and possibly elimination of TP glands, is required to give *lönnbergi*. No evi-

denee has been found of any tendency to eliminate the remaining pair of ancestral spermathecae. On the contrary, such variation as has already been recognized seems indicative of increase in size of battery by addition of a further pair opening at 11/12, a change that already has been made in other evolutionary lines.

In evolving from its common ancestor with *lönnbergi, carolinensis* has acquired a different kind of pigment, eliminated the last of the original pairs of spermathecae, eliminated (or reduced) the GS glands as well as the TP glands if the latter had not been lost previously, and shifted the tubercula into xxvii-xxix.

Tubercula, in xxvi-xxviii in *lönnbergi,* xxvii-xxix in *carolinensis,* xxviii-xxx or less often xxviii-xxxi in *foetida,* xxix-xxxi in *rosea,* xxx-xxxi in *hortensis,* xxxi-xxxiii in *octaedra,* provide an interesting sequence. Though the series may be indicative of the way evolution has proceeded it does not, in this case, evidence phylogenetic relationships. Transfer of *rosea* from *Eisenia* to some other genus, as already mentioned, is necessary. American endemics may not be congeneric with the European forms to which they seem to be most closely related. The transatlantic species, having lost calciferous lamellae in x, and the hearts of vi, are more advanced but organs that have been left out of consideration in the past are suggestive of long divergent lineages. Thus, *hortensis,* which has retained atrial glands after loss of atria as well as the coelomic TP glands, now appears to be older than *foetida,* in which both kinds of glands have been lost. *D. octaedra,* which has retained atrial and TP glands, except in advanced stages of infrasubspecific morph evolution, then would be older than *hortensis* as spermathecae still must be developed at levels determined by location of a particular rank of setae. Female pores, like the spermathecal pores, are more dorsal than in many lumbricids but because of shift in the *b* rank in association with which the oviducts seem obliged to acquire their external openings.

Abortion of hearts in x-xi of *octaedra,* except for vestiges in a rare individual, has been completed. Presence of hearts in xii has been recorded in an occasional lumbricid species but all such instances require confirmation because of known misidentifications of large vessels connecting extra-oesophageal and dorsal

trunks. Behind xi, in the Lumbricidae as in the Ocnerodrilidae, hearts probably have been developed rarely, if ever. A supra-oesophageal trunk seems never to have been developed in the Lumbricidae. Latero-oesophageal and oesophageal hearts are therefore impossible; all are lateral.

The geographical ranges of our native forms are as yet little known, earthworms having been collected mostly in and around municipal centers, farmyards, golf courses, etc., where introduced exotics are most likely to be found. Considerable approximation to extermination of endemics in competition with the intruders certainly seems to have been implied by Smith (1928). His conclusions, according to one of his graduate students (verbal communication) who secured many of the Illinois specimens mentioned in that contribution, were largely based on material from urban areas and banks of streams contaminated by sewage and industrial wastes. The influence of man, on the competition he has been responsible for initiating, certainly ought to be investigated in other sorts of habitats. Meanwhile, species of *Eisenia* apparently are to be sought in often neglected niches by stream banks and swamps, in forests and especially perhaps in the mountains of the Appalachian chain. The distributional ranges as now known, except for very recent colonization in the extreme southwest of New England, extend from New Jersey into Louisiana and are south of the limit of glaciation. Paucity of endemics of *Eisenia* in the vast area of North America may, then, be due, in part, to extinction of other species during the last glacial period. A similar paucity of species in Eurasia, where several different phylogenetic lineages (instead of one) now seem to be required, likewise may have resulted, in part, from ice age extermination.

A score or more of lumbricids, mostly of European origin, have been carried to almost every part of the world and to many places very many times, since the days of Henry the Navigator. Some (cf. Gates, 1954, p. 255) have become established, even widely distributed, in remote regions where they would not have arrived unaided. Intentional introductions of several of the most successful of the colonizing species have, however, often failed and the characterization of "cosmopolitan" (cf. Cernosvitov and Evans, 1947; Muldal, 1952) is unwarranted, probably for any lumbricid. Only thirteen individuals, all of a

single and possibly American species, were secured during a four year survey (Gates, 1945, 1947, 1956a) of the earthworm fauna of the Allahabad sector of the Gangetic valley and an adjacent area to the south from which more than 50,000 specimens were identified. Furthermore, a thirty-year study of the earthworms of southeast Asia showed that in spite of frequent introductions, intentional and accidental, lumbricids have not been able to maintain themselves where climate is tropical. Only in hill resorts at elevations of more than four thousand feet, in peninsular India, Burma and the Malay Peninsula, has there been some successful colonization. To find lumbricids elsewhere, it is necessary to go well above the tropics, even north of the Gangetic and Brahmaputra valleys into the eastern Himalayas. There, and again so far as is now known, in and around centers of European influence (Gates, 1951), endemics probably have been replaced by exotics some of which, however, are megascolecid. Indigenous lumbricids can be expected only in the western Himalayas and the far northwestern corner of India. Whatever the nature of the restriction, even the most successful of the colonizing lumbricids now appear to be limited to temperate zone types of climate. The less adaptable American endemics, in past ages, may then have been similarly prevented from establishing themselves in tropical portions of the continent.

SUMMARY

American species of *Eisenia* are closely related, obviously "good," and clearly distinguishable from their European congeners. The latter, in accordance with newly proposed evolutionary sequences based on characters hitherto unrecorded or neglected, now appear to be more advanced. Paucity of species on the American continent is attributed to inability to colonize in tropical climates, and to ice-age extinctions.

Lumbricid genera of the classical system now appear to be mostly congeries of species associated because of relatively recent and superficial convergences acquired at species or, sometimes, even lower levels. Genera must be redefined and by reference to more conservative organs less liable to rapid change during infrasubspecific evolution.

VII

Bimastos zeteki Smith and Gittins 1915

Highlands, North Carolina. In leaf mould and sandy soil (pH *ca.* 5.0) near path leading up to Whiteside Mountain, at altitude of *ca.* 4500 ft., August 21, 1932, 2-0-1. Dr. G. E. Pickford. In moderately damp, loamy soil by path to Primeval Forest, at altitude of *ca.* 3900 ft., July 24, 1931, 0-1-0. J. M. Valentine per Dr. G. E. Pickford. In pocket of sandy black soil (pH 5.0) under dead leaves by stream near path to Primeval Forest, July 25, 1931, 0-0-1. Dr. G. E. Pickford.

Linville, North Carolina. In earth (pH between 5.0 and 6.0) and leaf mould by stream in ravine at 4000 ft., on road to Blowing Rock, July 31, 1931, 0-0-4. Dr. G. E. Pickford.

Indian Gap (now Newfound Gap), Tennessee. In loamy soil (pH 5.0) among rotten wood by stream at *ca.* 4500 ft., near road and *ca.* 500 ft. below gap (Great Smoky Mountains), July 30, 1931, 0-0-9. Dr. G. E. Pickford.

Mt. Carmel, Connecticut. In rotten log, April 14, 1946, 0-0-1. Dr. G. E. Pickford.

Whitetop Mountain, Virginia. Under bark of log at elevation of 4700 feet, August 17, 1955, ?-0-1. Prof. Walter Harman. (15 small juveniles, or some of them, may be of this species.)

Mountain Lake, Virginia. Leaf mould at reservoir of Biol. Sta., June 20, 1955, 0-0-3. Sawdust pile, Castle Rock, July, 1955, 16-0-0. Castle Rock; August 12, 1955, 24-0-0, August 2, 1955, 0-1-0. Prof. Walter Harman.

Culver, Indiana, June 19, 1914, 0-0-2. H. V. Heimburger. (U. S. Nat. Mus. No. 26,214. Examined by courtesy of Dr. Fenner Chace.)

External characteristics. Length of worms not obviously amputees, 73-99 mm. (Carolina, Tennessee), 95-100 mm. (Indiana, relaxed?), to 135 mm. (Virginia, not relaxed). Diameter, 4 mm. (Indiana), 5-8 mm. (others). Segments, 126-154 (cf. Table 5), 135 (Indiana). Pigmentation unrecognizable in old (1914-1946) specimens and in formalin as well as in alcohol preservation. A red color, in old formalin material, usually is present in epidermis of the region between xv and the clitellum. The color may be lacking on xvi-xvii, indistinct or slight and then equatorial in the dorsum only. The colored band becomes wider posteriorly until intersegmental furrows are nearly reached and continuous around the ventrum, finally becoming indistinguishable from the clitellum. Pigmentation red, in recently preserved Virginia worms, in circular muscle layer and at both ends of

the body also in an outer portion of the longitudinal musculature. The color gradually disappears ventrally in *BC*, except in first and last few segments where the ventrum is red, and may be sparse except at mD in dorsum of probable clitellar region in largest juveniles. The body tends to be four-sided posteriorly though the dorsum, slightly wider than the ventrum, remains slightly convex. Prostomium epilobous, tongue open or closed (3 specimens, but adventitious?). Setae begin on ii on which all usually are present, one pair at each angle of the body posteriorly where $CD <$ or ca. $= AB$, $BC < AA < DD < \frac{1}{2}$C. Nephropores first recognizable on iii, usually close to or above *D* on anterior segments, posteriorly lateral to *B* (between levels of male and female pores) or in *DD*, sometimes well above *D*, without regular alternation and often at different levels on opposite sides of a segment. Both situations, with or without symmetry, have been found on xiv-xvi. Pores of six consecutive segments occasionally may be at one level on one side in the intestinal region but in each worm the pores on opposite sides of the same segments alternate between the two positions. First dorsal pore on 4/5 (1), ?5/6 (3), 5/6 (59), 7/8? (1).

Female pores equatorial, closer to *b* than *a* is, on xiv. Male pores each in a small, shallow, transversely slit-like depression in median half of *BC*, equatorial on xv.

Clitellum red (old formalin specimens) or white (old alcoholic and recent formalin material), saddle-shaped or annular, located as shown in Table 4. Tubercula pubertatis lacking (all).

Genital tumescences lacking or so slightly developed as to be almost unrecognizable. The *a-b* setae of certain segments are retracted, the margin of each follicle aperture tumescent, the annulus so small as to be easily overlooked. Genital tumescences, as so indicated, are on xvi (16 Carolina and Tennessee worms, 1 from Whitetop Mt., Virginia, possibly also in several small juveniles from the latter locality), on xxvii (6), xxvii-xxviii (11), xxvi-xxviii (1), all from Mountain Lake, Virginia. Male pore tumescences are small, scarcely or only slightly protuberant, confined to xv, sometimes (old formalin material) indicated merely by an epidermal translucence that does not reach either 14/15 or 15/16.

Internal anatomy. Septa 7/8-9/10 and 12/13-14/15 (especially 13/14) rather generally are muscular and thicker than 10/11-

11/12, 10/11 the thinner, but none is, compared to size of body, very much thickened. Longitudinal musele band at mD of freshly preserved material has a pink color. Peritoneal pigment flecks are lacking. Epidermis at parietal incisions of recent formalin material perfectly white as is circular musculature just underneath intersegmental furrows.

Calciferous gland extends well into x, often reaching nearly to 9/10 but only apparently, usually much wider in x, and then with an appearance as of a pair of vertical sacs. Constrictions at 10/11 and 11/12, when recognizable, are slight, but that in region of insertion of 12/13 and usually internal on both sides is marked. The gut lumen through the gland (x-xii) may be only a vertical cleft or wider and then variously so, sometimes wider than wall of gut. Oesophagus narrowed through xiii-xiv. Intestinal origin in xv (25). Gizzard in xvii-xviii (25), the layer with brilliant muscular sheen obviously extending somewhat behind insertion of 17/18 in horizontal sections but not reaching that of 18/19. Gut narrowed in xix and valvular at 19/20. Typhlosole, beginning gradually or more abruptly in region of xxii-xxvi, 1½-2 mm. high, reaching to or nearly to floor of gut, shape as in *Eisenia lönnbergi* Michaelsen 1894, often with a deep longitudinal groove on ventral face of largest portion (anteriorly), ending abruptly or otherwise as shown in Table 4.

Subneural trunk usually large and filled with blood (occasionally quite unrecognizable), adherent to cord, continued forward to subpharyngeal ganglia. Extra-oesophageal trunks turn upward posteriorly in xii to dorsal trunk, the vertical portion often distended with blood and looking much like a heart. A slender posterior continuation behind the upward curve is shortly recognizable only rarely. A branch of the extra-oesophageal, as large as the vertical portion in xii, passes upward in ix (several worms), through 9/10 and to the dorsal trunk just in front of the calciferous gland. From the subneural a large branch passes out in xii, xiii or xiv, on one or both sides, to join the extra-oesophageal in xii just as the latter turns up. The whole subneural trunk sometimes appears to turn out to one side to the extra-oesophageal but a slender continuation usually is recognizable further forward on the cord. The dorsal trunk gives off four large branches to the calciferous gland in x, two anteriorly, the others under the hearts. The trunk is empty

anterior to 6/7 (all), quite small, unrecognizable in front of 5/6 though probably not ending there. Hearts or commissures were not found in v-vi. Hearts of vii often rather small and empty. Last hearts in xi (25). Nephridia have been definitely identified only from iii posteriorly (present in ii?). Nephridial ducts pass into parietes at *B*. Brain, the posterior margin deeply incised, left in iii by a transverse section exactly along 3/4. Median, longitudinal groove in roof of pharynx in iv in cross section Y-shaped.

Seminal vesicles two pairs, in xi-xii (25), not rudimentary but rather small to quite small, in dorsal half of segment or between upper face of gut and dorsal parietes. Male funnels crenellate, small, often only two to three times the size of the nephridial funnels just beneath them, somewhat larger in the Indiana worm, with some opacity (usually) or translucent. Male deferent ducts slender, just behind funnel septa straight, sinuous, zigzag looped or loops (various) held together by connective tissue in a small flat disc, visible on parietes (southern worms) into xv. Spermathecae lacking (25) and rudiments unrecognizable in parietes after stripping off longitudinal musculature. Oviducts pass into parietes anterior to eq/xiv. Ovisacs, always present (25), may be of about the same size as the ovaries and slightly lobed.

Atrial gland nearly circular, flattened against parietes, crossed by an equatorial cleft, another cleft at insertion of 16/17, the gland extending into xvi (19).

Follicles of the ventral setae in xv-xxxviii usually appear to be slightly larger than those of the lateral setae in the same segments. None of them, in the Indiana worm, appear to be especially enlarged. Special enlargement in other specimens is associated with the external modifications already mentioned. GS follicles of xvi are surrounded on the parietes by an acinous glandular mass or the lobules may be present only on posterior and median sides. No such glands are recognizable in posterior segments.

Juveniles. Atrial glands are lacking in worms as large as 110 x 8, 125 x 6 mm., even in one 135 mm. long, but without any recognizable epidermal tumescence in presumed clitellar region. GS follicles are, however, protuberant into coelom and modifications around the follicle apertures are recognizable. Associated glands are not yet recognizable in the coelom. Enlargement of

setal follicles may be recognizable in much smaller juveniles on some of which rudiments of male pores and their tumescences are not yet detectable.

Abnormality. Metamerism is abnormal in one or more regions of a posterior portion of the body in two worms.

Regeneration. An anal segment had been reconstituted in each of the posterior amputees. No other regeneration had taken place though amputation in some of the cases certainly had not been recent. Posterior regeneration, as in *Lumbricus terrestris* L., may not be possible in ordinary conditions.

Parasites. Large, thin-walled cysts with a watery content (2-6 per segment in coelomic cavities of x-xi) were present in seven Carolina-Tennessee worms in one of which each of the unusually large seminal vesicles contained 2-4 more of the cysts. Further cysts of the same sort were present in the coelom of the last fifteen segments of one worm, along with much smaller opaque spheroidal bodies. The latter were scattered through the postclitellar portion of the body of several worms but were especially numerous in the last few segments of posterior amputees along with "brown" bodies, some of which were white.

Life history. Clitellar tumescence had become unrecognizable in a July worm but the site of the clitellum was indicated by the usual postreproductive discoloration. Full clitellar tumescence may not have been attained by several July worms in which intersegmental furrows still were faintly visible on the dorsum or in which acinous glands around GS follicles still were very small. The clitellum of the April and some July specimens was at or near maximal tumescence. Three spermatophores on one of the Carolina-Tennessee worms are firmly attached to xxviii just lateral to *B* and in *CD* and to xxv at mV. Each is a transparent flattened, nearly square disc containing centrally a rather small ellipsoidal to ovoidal white body.

The breeding season, judging from clitellar development, spermatophores, etc., would seem to include April in Connecticut, June in Virginia, July in the mountains of Tennessee and North Carolina. During June, in Indiana, cocoons were found according to Heimburger (1915, p. 285) and worms were at "height of sexual maturity." Material that would provide evidence as to a fall breeding season has not been available.

No spermatozoal iridescence was recognized on male funnels of any worm including one from Indiana, nor in the opaque central bodies of the spermatophores. Male funnels are not of normal size and development in some of the worms. Seminal vesicles are of about the same small size in some worms with maximal clitellar tumescence as in the postsexual aclitellate and in juveniles. The largest seminal vesicles are merely membranous sacs filled with cysts. The worms, if deductions as to breeding season are correct, are male sterile in which case reproduction must be parthenogenetic.

Remarks. The red color of the epidermis from xv-xxvi, like that of the clitellum, presumably is a formalin-developed artifact but must indicate, because of constant localization, some chemical difference from other regions. The difference probably is established at maturity and the change must be reversible during postreproductive regression as the color was lacking in the regressed aclitellate worm. The brown of the "purplish-brown" coloration mentioned by Smith (1917, p. 175) may have been a product of postreproductive metabolic changes.

The clitellum in this species, according to the original description, covers 11 or 11½ segments, xxvii-xxxvii or eq/xxvii-xxxviii. Only xxvii-xxxvii is mentioned by Smith in his subsequent characterization of the species (1917) though he had "considerable numbers" of worms from three states. No further data have been provided subsequently by authors who recorded *zeteki* from New York, Ohio, Indiana, Michigan, Missouri, Arkansas, Louisiana and North Carolina. In absence of such data it should be assumed that the clitellum was on xxvii-xxxviii in material from all of those localities since location of that organ has been about the only character used for routine identification of species of *Bimastos*. However, no single individual herein considered has a clitellum exactly on xxvii-xxxvii. Anterior and posterior margins both appear to be rather indistinct often, due to a gradual rather than the usual abrupt decrease in epidermal thickness. At present it seems that the clitellum may cover nine to fourteen segments, beginning at or behind 25/26 and ending between 35/36 and 39/40. Location of anterior margin at or behind 25/26 seems to be about the only character now available to distinguish *zeteki* from *longicinctus* Smith and Gittins 1915.

GS follicles have not been recorded hitherto. They may have

been lacking in Illinois and Indiana worms. If so, two other strains may be recognizable, one with follicles in xvi (or xv-xvi) only and associated with acinous glands, another having the follicles more posteriorly, in the region of xxvi-xxviii, but no glands. Strain ii (Carolina to Virginia), with acinous glands such as are present in the sexual *palustris*, may be the most primitive. Strain iii (Mountain Lake, Virginia) without acinous glands, then would be more advanced and i (Indiana, Illinois?) the most advanced. The latter is the one nearest to the southern limit of the recent glaciation.

Parthenogenesis is suspected in two other species of *Bimastos* (cf. III-V), *tumidus* and *parvus*, and in the latter may in part have been responsible for colonization of various extra-American regions, but has not been similarly advantageous to *zeteki*.

Spermatophores must have been developed, in the ancestry of *zeteki*, before spermathecae were eliminated. They still can be produced and presumably are attached to the surface of the body during a futile copulatory act (pseudocopulation). The male sterility could have become established in this form only after modification in oogenesis to permit parthenogenesis.

Table 4

Clitellar characteristics in *Bimastos zeteki*

	Clitellum on segments	Shape	Tumescence	Locality	Epidermis red on segments
1.	26-35(?)*	?	0	Highlands	0
2.	26-35	A	medium	Highlands	?
3.	26-35	A	maximal?	Linville	17-25
4.	26-35	A	marked	Indian Gap	16-25
5.	26-35	A	marked	Indian Gap	16-25
6.	26-35(36?)	S	medium	Indian Gap	24-25 + VC
7.	26-35(36?)	A	maximal?	Indian Gap	(17 18?) 19 25
8.	26-35(36?)	A	marked	Indian Gap	16-25
9.	26-36	A	marked	Linville	17 25
10.	26-36	A	maximal?	Linville	17-25
11.	26-36	A	marked	Indian Gap	17-25
12.	26-36(37?)	S	medium	Indian Gap	0 VC
13.	eq/26-36/eq	A	marked	Indian Gap	17-25
14.	eq/26-36/eq	A	marked	Highlands	17-25
15.	(26-27)28-37(38-39)	S	marked	Mt. Carmel	?
16.	27-35(36?)	A	maximal	Indian Gap	17-25
17.	26-35	S	maximal?	Whitetop Mt.	
18.	(26?)27-37(38?)	S	maximal?	Virginia	
19.	(26?)27-38/eq	S	maximal?	Virginia	
20.	(27?)28-37	S	maximal?	Virginia	
21.	27-38/eq	S	maximal?	Indiana	
22.	28-38/eq	S	maximal?	Indiana	

*Site of clitellum indicated by postreproductive discoloration.

A. Annular. S. Saddle-shaped. eq. Equator.

VC. Epidermis in *AA* as red as clitellum.

(36?) Epidermis of dorsum in xxxvi red, slightly thickened, decreasingly so anteroposteriorly.

(26-27) Epidermis red, increasingly thickened anteroposteriorly in xxvi-xxvii but furrow 26/27 still visible.

Dorsal pores are occluded except in an early stage of clitellar development. Intersegmental furrows are obliterated as tumescence becomes marked but even when clitellum is annular still are slightly indicated in *BB* or *AA* according to degree of tumescence. Setae and nephropores retained.

Thickening of epidermis in *AA* or *BB* in worms with a supposed saddle-shape of clitellum, might have been recognizable in sections.

TABLE 5

Typhlosole termination and segment number in *Bimastos zeteki*.

Typhlosole ends in segment	Atyphlosolate segments	Number of segments	Locality	Remarks
76	18	94	Highlands	amputee
80	16	96	Linville	amputee
84	16	100	Indian Gap	amputee
85	22	107	Highlands	amputee? juvenile
87	20	107	Indian Gap	amputee
89	11	100	Whitetop Mt.	amputee?
96	33	129	Highlands	
97	2+	99+	Indian Gap	Broken off posterior end lacking
97	29	126	Indian Gap	amputee?
98	28	126	Linville	
100(±1-2)	40	140(±1-2)	Linville	
101	30	131	Indian Gap	
103	45	148	Linville	
104	35	139	Indian Gap	
104	37	141	Mt. Lake, Virginia	
104	42	146	Indian Gap	
104+	?	104+	Indian Gap	Broken off posterior end lacking
103-106	43-46	149	Mt. Lake, Virginia	
106	38	144	Highlands	juvenile
106	45	151	Mt. Lake, Virginia	
97-107	15-25	122	Mt. Lake, Virginia	
104-108	20-24	128	Mt. Lake, Virginia	
108	44	152	Indian Gap	
109	29	138	Highlands	amputee?
109	33	142	Mt. Carmel, Conn.	
110	44	154	Mt. Lake, Virginia	

(±1-2) Anterior end which had been broken off in front of clitellum was lacking.
103-106 Typhlosole terminates very gradually, rather than abruptly, exact end of the organ uncertain.

Posterior amputation of long standing may be unrecognizable because of reorganization of last segments. Number of segments in "complete specimens", according to Smith (1917, p. 175), usually 130. The maximum he mentioned, 142.

DISCUSSION

The genus *Bimastos* was erected for a single American species, *palustris* Moore 1895, which lacks tubercula pubertatis, seminal vesicles in ix-x, as well as spermathecae. The genus shortly became (cf. Michaelsen, 1900) a taxonomic waste-basket into which similarly defective forms, regardless of morphology and geographical distribution, were thrown. One of those so misplaced is *Allolobophora tenuis* Eisen 1874 which occasionally has one to three, more or less rudimentary spermathecae as well as more or less indistinct markings assumed to be tubercula. Because of a "tendency" to develop spermathecae, Smith (1917, p. 178) suggested that an admittedly confused taxonomy could be somewhat simplified by tranfer of *tenuis* to *Dendrobaena* Eisen 1874 which has spermathecae. Actually, most specimens of *tenuis,* as long suspected (cf. Gates, 1953, p. 531, footnote), have been of an A morph of *D. rubida* (Savigny, 1826), the individuals with more or less rudimentary spermathecae being "intermediates" in which elimination of spermathecae has not yet been completed (cf. Gates, 195?c). *D. rubida* obviously is exotic in America. Other Eurasiatic A morphs that have been erroneously referred to *Bimastos* may prove to be capable of similar association with a normal H morph, when intermediates have been found if not before. The finding of H morphs of the various American species of *Bimastos* cannot now be anticipated as the only other endemic lumbricids are distinguishable at generic level.

REFERENCES

Černosvitov, L. and A. C. Evans

1947. Lumbricidae. Linnean Soc. London, Synopses British Fauna, **6:** 1-36.

Davies, H.

1954. A preliminary list of the earthworms of northern New Jersey with notes. Breviora, **26:** 1-13.

Gates, G. E.

1943. On some American and Oriental earthworms. Ohio Jour. Sci., **43:** 87-116.

1945. The earthworms of Allahabad. Proc. Nat. Acad. Sci. India, **15:** 45-56.

1947. Earthworms of the Allahabad sector of the Gangetic plain. Proc. Nat. Acad. Sci. India (B), **17:** 117-128.
1951. On the earthworms of Saharanpur, Dehra Dun, and some Himalayan hill stations. Proc. Nat. Acad. Sci. India (B), **21:** 16-22.
1953. On the earthworms of the Arnold Arboretum, Boston. Bull. Mus. Comp. Zool., Harvard, **107:** 500-534.
1954. Exotic earthworms of the United States. Bull. Mus. Comp. Zool., Harvard, **111:** 219-258.
1955. Notes on American earthworms of the family Lumbricidae. I-II. Breviora, **48:** 1-12.
1956a. Earthworms of the region south of the Allahabad sector of the Gangetic plain. Proc. Nat. Acad. Sci. India (B), (in press).
1956b. The earthworms of Burma. VII. The genus *Eutyphoeus*. With notes on several Indian species. Rec. Indian Mus. Calcutta, (in press).
1956c. Reproductive organ polymorphism in earthworms of the oriental megascolecine genus *Pheretima* Kinberg 1867. Evolution, (in press).

HEIMBURGER, H. V.
1915. Notes on Indiana earthworms. Proc. Indiana Acad. Sci., 1914: 281-285.

KOBAYASHI, S.
1940. Terrestrial Oligochaeta from Manchoukuo. Sci. Rep. Tohoku Univ., (4) **15:** 261-315, figs. 1-15.

MICHAELSEN, W.
1900. Oligochaeta. Das Tierreich, **10.**

MOORE, H. F.
1895. On the structure of *Bimastos palustris*, a new Oligochaete. Jour. Morph., **10:** 473-496, pls. 26-27.

MULDAL, S.
1952. The chromosomes of the earthworms. I. The evolution of polyploidy. Heredity, **6:** 55-76.

OMODEO, P.
1952. Cariologia dei Lumbricidae. Caryologia, **4:** 173-275.
1955a. Lombrichi cavernicoli di Grecia e Turchia raccolti dal Dr. K. Lindberg. Ann. Ist. Zool. Univ. Napoli, **7:** 1-16.
1955b. Aspetti biogeografici della speciazione. Boll. Zool., **21** (2): 1-56.

PICKFORD, G. E.
1937. A monograph of the acanthodriline earthworms of South Africa. Cambridge, England.

POP, V.
1941. Zur Phylogenie und Systematie der Lumbrieiden. Zool. Jahrb. Syst., **74:** 486-527.

SMITH, F.
1917. North American earthworms of the family Lumbrieidae in the collections of the United States National Museum. Proc. U. S. Nat. Mus., **52:** 157-182.
1924. The calciferous glands of Lumbricidae and Diplocardia. Illinois Biol. Mon., **9** (1): 1-76.
1928. An account of changes in the earthworm fauna of Illinois and a description of one new species. Bull. Illinois Nat. Hist. Survey, **17:** 347-362.

STEPHENSON, J.
1930. The Oligochaeta. Oxford.

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 115.

Breviora (octavo) 1952 — No. 57 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899-1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 115, No. 2

A QUANTITATIVE STUDY OF THE EQUIDAE OF THE THOMAS FARM MIOCENE

By Robert S. Bader

University of Florida

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
August, 1956

No. 2—*A Quantitative Study of the Equidae of the Thomas Farm Miocene*

By Robert S. Bader

INTRODUCTION

The most important terrestrial vertebrate locality in the Tertiary of eastern North America is the Thomas Farm of north central Florida. More terrestrial mammalian species have been described from this Gilchrist County Miocene locality than from any other Tertiary deposit east of the High Plains. A general review by Romer (1948) includes a complete bibliography of the work to that date. Since 1948, additional herpetological remains have been described by Tihen (1951), Vanzolini (1952), Williams (1953), Goin and Auffenberg (1955), and Auffenberg (1956). A new bird genus has been described by Brodkorb (1954).

The most abundant species occurring at this site are included in the Equidae, especially in the genus *Parahippus*. These assume primary importance not only because of their frequency of occurrence but also because of the critical stage of equid evolution which they represent. This most interesting and crucial phase in the history of the family was marked by an increase in gross size, in hypsodonty and in the intricacy of the dental pattern, as well as by the appearance of cement on the teeth. Coincident with, and inferentially in consequence of, these widespread morphological changes there occurred an equally momentous ecological shift from a browsing to a grazing habitat. Subsequent to the last detailed discussion of the horses (White, 1942), the accruement of material has been considerable (primarily through the efforts of the Museum of Comparative Zoology; recently, collections have been made for the University of Florida by the author). Because of this fact and since the large collection is amenable to statistical analysis, a quantitative study was undertaken in the hope of shedding new light on the relationships of the several species previously described.

Simpson (1932) recognized 3 species from the earlier Miocene

deposits of Florida: *Archaeohippus nanus* Simpson from the Thomas Farm, *Parahippus leonensis* Sellards (1916) type from a well on the Griscom Plantation near Tallahassee and referred specimens from Thomas Farm, and *Anchitherium clarencei* Simpson, type from Midway, also near Tallahassee, and referred material from Thomas Farm. White (1942), with a much more extensive series at his disposal than was available to Simpson ten years earlier, recognized seven species from Thomas Farm, viz., *Miohippus* sp., *Parahippus blackbergi, Parahippus barbouri, Parahippus leonensis, Merychippus gunteri, Anchitherium clarencei,* and *Merychippus westoni.* The last named species, found near Newberry, (Alachua County), Florida, and described by Simpson (1930), was not identified with certainty by White and none of the more recent material can definitely be assigned to it. A lower jaw was referred to *A. clarencei* by White in addition to the material described earlier from this locality by Simpson (1932). Although there is no doubt that this large, conservative form did occur at Thomas Farm, more recent collecting has failed to reveal any new material of it.[1]

The great bulk of the equid material is composed of representatives of the four remaining species recognized by White, and it is principally with these that the present study is concerned. *P. blackbergi* was originally defined on the basis of material from the Garvin Gulley, Texas, and placed in *Miohippus* by its author, Hay. It was assigned to *Archaeohippus* by Stirton (1940) in his general review of the family. As mentioned above, Simpson described a new species, *A. nanus*, from the Thomas Farm material available to him in 1932, but White (1942) referred to this form as *P. blackbergi*, placing *A. nanus* in synonymy. *P. barbouri* was described by White from the Thomas Farm, and *M. gunteri* by Simpson (1930) from Midway. White considered these four species to represent a phyletic series in the following manner: *P. blackbergi* ⇒ *P. barbouri* ⇒ *P. leonensis* ⇒ *M. gunteri.* This evolutionary sequence, spanning the morphological range between a very primitive *Parahippus* and a very primitive *Merychippus,* in his view presumably occurred *in situ* in the Thomas Farm area.

[1] A first median phalanx has been found in the clay below the boulder bar on the north face of the quarry since this was written.

ANALYSIS

A tabulation of the total number of associated dentitions measured is given in Table 1. The total sample is seen to include over 200 specimens, many of which were, of course, incomplete. Numerous isolated teeth also occur in the collections; however,

TABLE 1.

Parahippus blackbergi	Permanent	Deciduous
uppers	23	2
lowers	23	1
Total	46	3
P. barbouri, P. leonensis, Merychippus gunteri		
uppers	61	6
lowers	82	9
Total	143	15
Grand Total	189	18

Table 1. A tabulation of the total number of associated dentitions measured in the study.

since P^3 and M^1 often could not be distinguished with certainty from P_4 and M_1 respectively, they were not included in the statistics given below. Length, width, and height measurements were taken on all associated cheek teeth. Certain measures or counts (e.g., dimensions of the protoeone, metaeonid-metastylid and erochet and number of plications on the metaloph) were attempted and then abandoned. It was felt that statistics of such measures (and estimates of parameters derived therefrom) would add little to the classical procedures of description due to the inconsistencies introduced by the variation of these dimensions with wear, the nonhomologous nature of certain measures in different wear stages (e.g., width of protocone), and the inability to repeat measures within satisfactory limits. All but the measuring error could be eliminated by treating only specimens exhibiting little or no wear. Such an analysis, however, would be limited to only a small percentage of the total and would thus largely nullify the most attractive feature, from an evolutionary point of view, afforded by the Thomas Farm material, i.e., the opportunity to study evolving populations.

The use of tooth length as a valid measure perhaps requires some defense since it is known to be influenced by wear and for

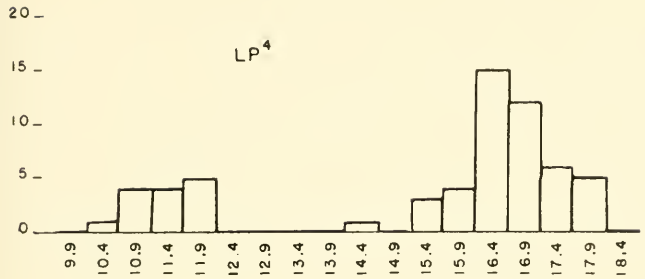
that reason it has not been regarded as reliable, at least by some students of the Equidae, in the sort of detailed comparison that is attempted here. Correlations and partial correlations of length, width, and height were calculated for various members of the dental series in both the larger and smaller population. The r values ranged from near+ .7 to almost 0, many of which were not significant. Part of the correlation of height and length must be attributable to the heritability of the dimensions involved, i.e., in unworn teeth, height and length would be expected to show a positive correlation since they are probably different phenotypic expressions of the same general genetic complex (in addition to which there may be factors for each trait). Width, not affected by wear as measured on these specimens, is a third manifestation of the same complex. Partial correlations of length and height (width held constant) almost invariably exhibited a lower value than the simple correlations between length and height. In other words, some of the correlation between height and length is caused by factors also common to width. These must be factors affecting general dental size (or perhaps gross size?) and cannot be attributed to the effects of age (wear). The convergence in many of the teeth is most striking a few millimeters above the enamel base, a point not reached by wear in almost all of the species studied. It may be assumed, from such evidence, that dental length may be used, at least in these forms, with relative impunity. Data obtained from coronal length follow essentially the same pattern as that of the widths and is thus susceptible to the same interpretation.

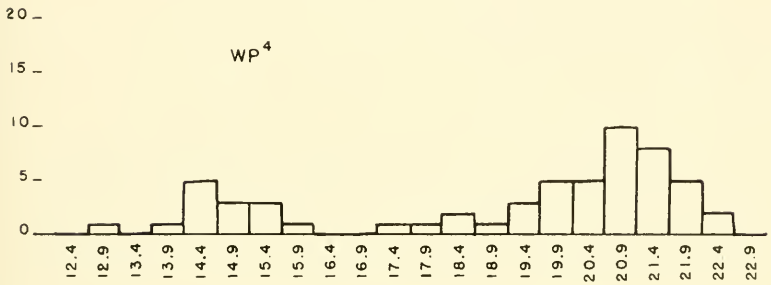
The measurements and their symbols are as follows:

Length of total cheek series (TCS) — the total length of the cheek series taken at the grinding surface.

Length of the cheek tooth (LP^2, etc.) — the maximum length of the ectoloph (or ectolophid) measured at the grinding surface.

Width of cheek tooth (WP^2, etc.) — Uppers: the maximum distance from the mesostyle to the lingual border of the protocone measured at the enamel base. Lowers: the distance from the protoconid to a point essentially midway between the paralophid and the metaconid, measured at the base and normal to the long axis of the tooth.


20
15
10
5
0
LP4
9.9
10.4
10.9
11.4
11.9
12.4
12.9
13.4
13.9
14.4
14.9
15.4
15.9
16.4
16.9
17.4
17.9
18.4


20
15
10
5
0
WP4
12.4
12.9
13.4
13.9
14.4
14.9
15.4
15.9
16.4
16.9
17.4
17.9
18.4
18.9
19.4
19.9
20.4
20.9
21.4
21.9
22.4
22.9

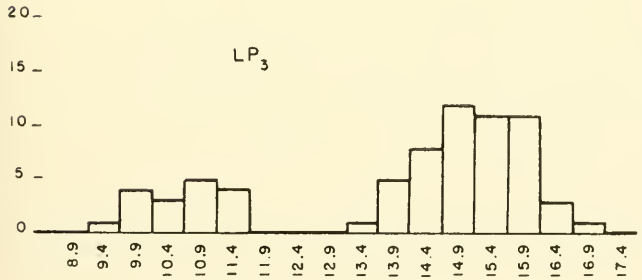

20
15
10
5
0
LP3
8.9
9.4
9.9
10.4
10.9
11.4
11.9
12.4
12.9
13.4
13.9
14.4
14.9
15.4
15.9
16.4
16.9
17.4

FIGURE 1

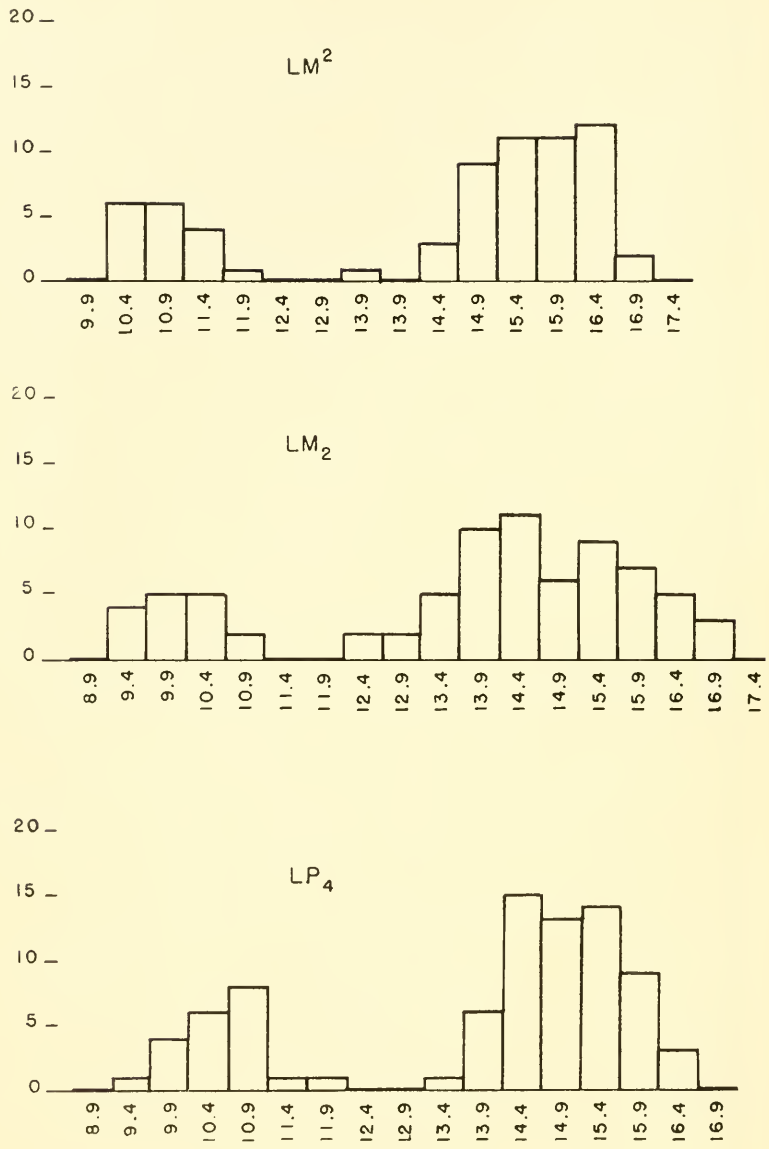

20
15
10
5
0
LM2
9.9
10.4
10.9
11.4
11.9
12.4
12.9
13.9
13.9
14.4
14.9
15.4
15.9
16.4
16.9
17.4
20
15
10
5
0
LM2
8.9
9.4
9.9
10.4
10.9
11.4
11.9
12.4
12.9
13.4
13.9
14.4
14.9
15.4
15.9
16.4
16.9
17.4
20
15
10
5
0
LP4
8.9
9.4
9.9
10.4
10.9
11.4
11.9
12.4
12.9
13.4
13.9
14.4
14.9
15.4
15.9
16.4
16.9

FIGURE 2

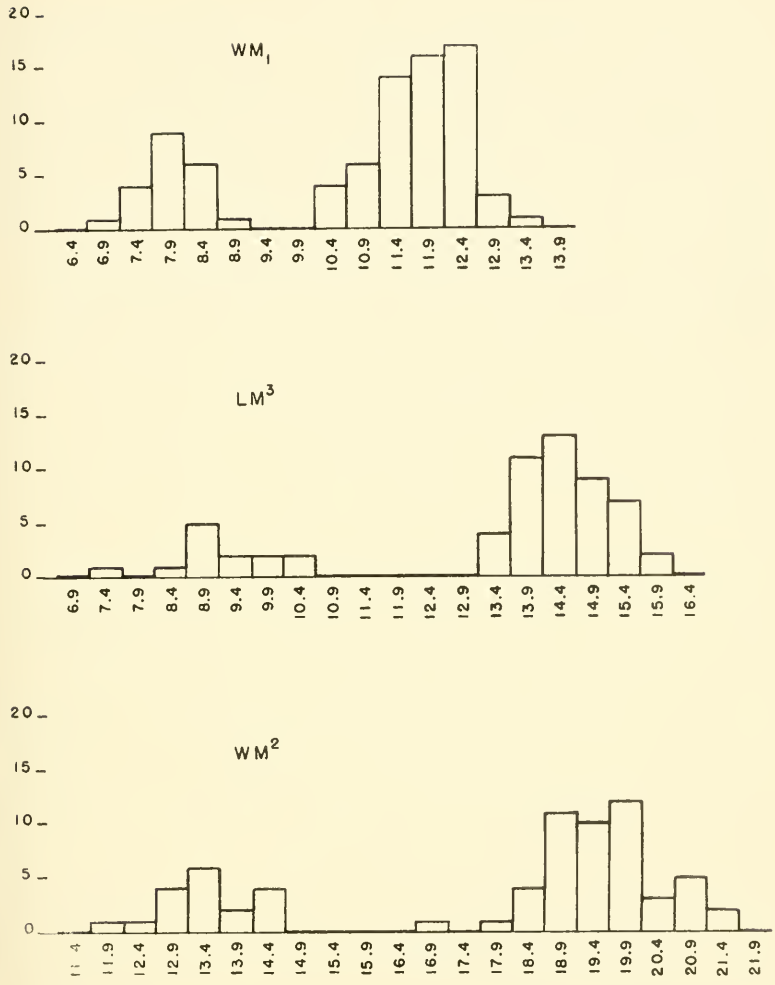


FIGURE 3

Figures 1-3. Frequency distributions of typical dental dimensions for the entire sample, including *Parahippus blackbergi*, *Parahippus barbouri*, *Parahippus leonensis*, and *Merychippus gunteri*. Class midpoints are plotted on the abscissae, frequencies on the ordinates.

Height of the cheek tooth (HP^2, etc.) — Uppers: from the tip of the mesostyle to the base of the enamel. Lowers: from the tip of the entoconid to the enamel base.

Frequency distributions were plotted for the length and for the width of both the upper and lower cheek teeth for the combined sample, a total of twenty-four distributions. Nine of these have been selected as typical and are presented in Figures 1 to 3. These distributions demonstrate fundamentally the same pattern irrespective of the dimension or tooth selected, i.e., there is a larger, more numerous population distinctly separable from a population smaller with respect to both dimensions and number of individuals. Only minor deviations from a normal distribution are in evidence, with little or no suggestion of bi- or trimodality in the larger group. The approximation to a normal curve is much closer for the larger assemblage, as would be expected from the relative sample sizes. An upper dentition (MCZ 3742) falls at about the 3σ limit for several characters and is usually almost a millimeter smaller than the next larger individual (Figs. 1 to 3). This specimen was referred to *P. barbouri* by White. Frequency distributions for two postcranial elements are given in Figure 4. The sample size is very large in both, numbering 338 for the calcanea and 552 for the phalanges. The same basic pattern as that of the dental elements is discernible here. The extremes of these variates in the two populations overlap slightly as seen from the grouped distributions; however, the ungrouped data show a hiatus of about 1 mm. in the calcanea distribution and of 0.3 mm. in that of the phalanges. The observed ranges, then, do not overlap, although the standard ranges do to a limited extent. Limited samples of several other postcranial elements were also available. Insofar as conclusions can be drawn from these small samples ($N \gtrless 30$), they appear to demonstrate basically the same features as those of the more numerous elements.

Scatter diagrams for several of the pairs of variates were plotted and three, selected as representative, are presented in Figure 5. On the basis of these ratios, the group is clearly separable into only two populations. The slope and position of regression lines is nearly the same in the two populations.

Sample size (N), mean ($\bar{x}$), observed range (O.R.), standard range (S. R. [S. D.]), standard deviation (σ), and coefficient of variation (V) for the dental dimensions of the two populations

are given in Tables 2 and 3. There is but slight overlap in the standard ranges for a few traits and none in the observed ranges. A most pertinent point relative to the present discussion is the magnitude of the variation in the respective populations. That the smaller population represents a single species is the unanimous opinion of all who have studied the group, a judgment with which the present findings are in agreement. The variation in this "good" species represents, therefore, the best available standard of comparison for the larger group. Although the material referred to *P. leonensis* alone, has been characterized as unusually variable, the variation in the odontometric traits of the total larger population from Thomas Farm (*P. barbouri,*

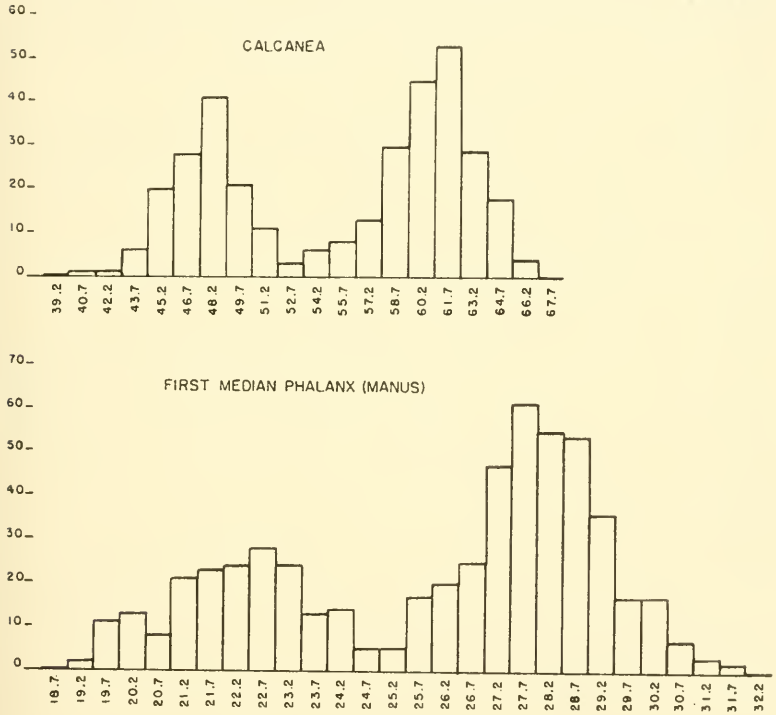


Figure 4. Frequency distributions of two postcranial elements for the entire sample. Class midpoints are plotted on the abscissae, frequencies on the ordinates.

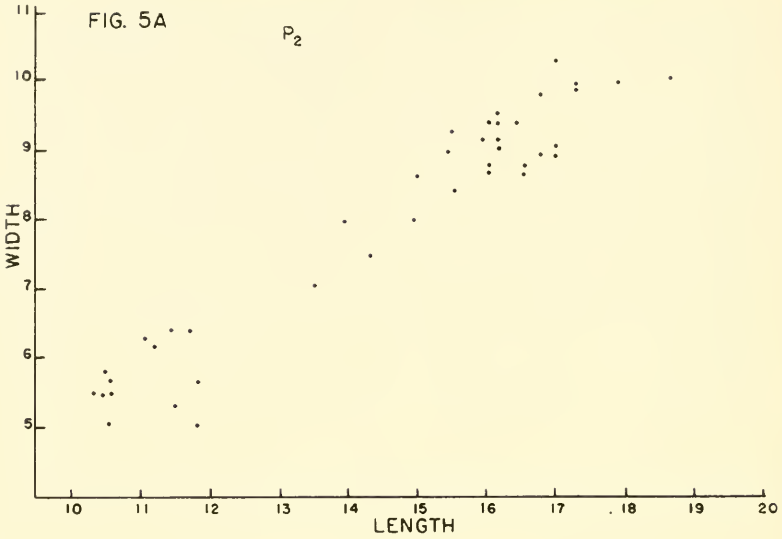


FIGURE 5A

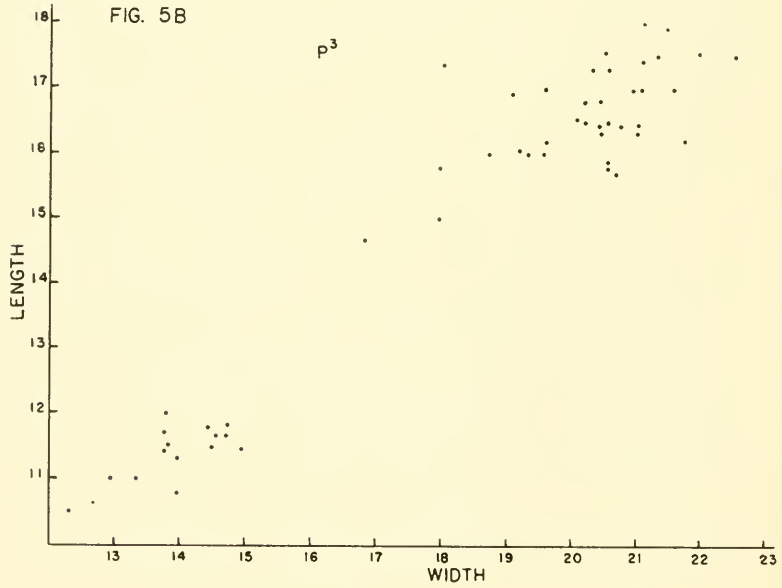


FIGURE 5B

P. leonensis and *M. gunteri*) is quite comparable to that of *P. blackbergi*. The mean V for the maxillary teeth is 5.06 in *P. blackbergi* compared to 4.98 in the larger population. The figures for the mandibular teeth are 5.64 and 5.88 respectively. The V's in each group are at or near the mode for homologous traits in both fossil and Recent mammalian species. Patently, on the basis of quantitative considerations alone, the total sample cannot be divided into more than two populations.

The maximum unworn height of the M^2 in *P. blackbergi* is about 10 mm. and approximately 16 mm. in the larger group. Seasonal deposition of the remains of animals which reproduce seasonally should result in a multi-modal distribution of a character which is highly correlated with age, e.g., the crown height of teeth. Matthew (1924) divided a large sample of *Merychippus*

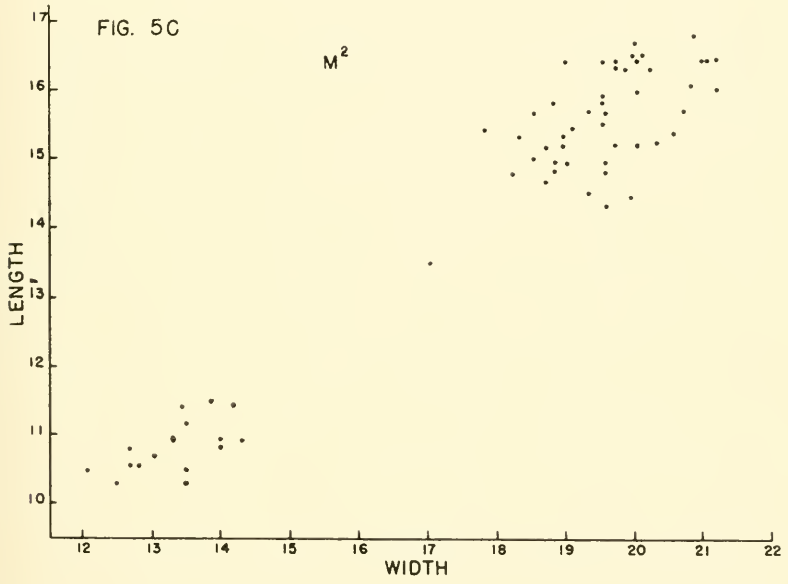


FIGURE 5C

Figure 5A, B, C. Scatter diagrams of coronal length and width for selected teeth. The total sample is included.

primus from the Snake Creek horizon into several distinct age groups based on eruption and wear of the molars. Kurten (1953) found a striking multi-modality in the distribution of molar height in several artiodactyls from the Pontian fauna of

TABLE 2

Variate	N	$\bar{X}$	O.R.	S.R. (S.D.)	σ	V
TCS	8	62.80 ± .97	58.6 - 66.2	53.9 - 71.7	2.74 ± .69	4.49 ± 1.09
LP^2	15	12.59 ± .14	11.6 - 13.4	10.8 - 14.3	.54 ± .10	4.33 ± .78
LP^3	17	11.44 ± .10	10.5 - 12.1	10.1 - 12.8	.43 ± .07	3.83 ± .65
LP^4	14	11.33 ± .13	10.4 - 12.0	9.8 - 12.9	.47 ± .09	4.25 ± .78
LM^1	16	11.61 ± .13	10.7 - 12.3	9.9 - 13.3	.53 ± .09	4.63 ± .81
LM^2	17	10.87 ± .10	10.3 - 11.8	9.5 - 12.2	.41 ± .07	3.83 ± .65
LM^3	13	9.19 ± .22	7.3 - 10.2	6.6 - 11.8	.79 ± .15	8.72 ± 1.68
WP^2	15	12.24 ± .16	11.0 - 13.0	10.2 - 14.3	.62 ± .11	5.16 ± .93
WP^3	15	13.95 ± .19	12.3 - 14.9	11.6 - 16.3	.73 ± .13	5.29 ± .95
WP^4	14	14.65 ± .20	13.0 - 15.7	12.3 - 17.1	.74 ± .14	5.11 ± .95
WM^1	13	14.01 ± .15	13.1 - 14.8	12.3 - 15.7	.52 ± .10	3.83 ± .73
WM^2	18	13.44 ± .17	12.1 - 14.6	11.1 - 15.7	.71 ± .12	5.32 ± .88
WM^3	13	10.99 ± .21	9.0 - 11.8	8.5 - 13.5	.76 ± .15	7.04 ± 1.36
TCS	9	64.68 ±1.02	60.5 - 68.6	54.8 - 74.6	3.05 ± .72	4.85 ± 1.11
LP_2	13	11.04 ± .16	10.3 - 11.8	9.2 - 12.9	.57 ± .11	5.28 ± 1.01
LP_3	17	10.64 ± .15	9.6 - 11.4	8.6 - 12.7	.62 ± .11	5.91 ± 1.00
LP_4	21	10.54 ± .13	9.8 - 11.8	8.3 - 12.8	.60 ± .09	5.77 ± .88
LM_1	20	10.13 ± .13	9.2 - 10.9	7.9 - 12.4	.60 ± .10	6.03 ± .94
LM_2	16	9.99 ± .13	9.2 - 11.1	8.3 - 11.7	.52 ± .09	5.25 ± .91
LM_3	12	10.80 ± .10	10.3 - 11.6	9.7 - 11.9	.34 ± .07	3.20 ± .64
WP_2	13	5.73 ± .13	5.1 - 6.4	4.2 - 7.2	.46 ± .09	8.27 ± 1.58
WP_3	17	7.39 ± .11	6.7 - 8.5	5.9 - 8.9	.47 ± .08	6.47 ± 1.09
WP_4	21	8.37 ± .10	7.7 - 9.4	6.9 - 9.9	.46 ± .07	5.50 ± .84
WM_1	21	7.96 ± .09	7.1 - 8.9	6.6 - 9.3	.41 ± .06	5.15 ± .79
WM_2	17	7.57 ± .10	6.9 - 8.3	6.2 - 8.9	.42 ± .07	5.61 ± .95
WM_3	13	6.50 ± .11	5.9 - 7.1	5.3 - 7.7	.38 ± .07	5.97 ± 1.14

Table 2. Dental statistics of the smaller population, *Parahippus blackbergi*. Symbols explained in the text.

China. It might be assumed that a similar distribution could be recognized in the Thomas Farm material since deposition is definitely of a seasonal nature now and probably was in the middle and late Tertiary. A study of both the limited samples of the

TABLE 3

Variate		$\bar{X}$	O.R.	S.R. (S.D.)	σ	V
TCS	21	92.35 ± .81	82.3 - 98.4	80.3 - 104.4	3.73 ± .58	4.09 ± .62
LP^2	33	19.56 ± .17	16.8 - 21.1	16.4 - 22.7	.98 ± .12	5.04 ± .62
LP^3	42	16.58 ± .12	14.4 - 18.0	14.1 - 19.1	.78 ± .09	4.74 ± .51
LP^4	46	16.65 ± .11	14.6 - 18.1	14.3 - 19.0	.73 ± .08	4.41 ± .46
LM^1	42	15.52 ± .14	12.9 - 16.9	12.7 - 18.4	.88 ± .10	5.72 ± .62
LM^2	49	15.58 ± .11	13.5 - 16.8	13.2 - 18.0	.74 ± .08	4.79 ± .48
LM^3	46	14.49 ± .09	13.3 - 15.7	12.5 - 16.5	.61 ± .06	4.24 ± .44
WP^2	34	18.37 ± .20	14.9 - 20.5	14.6 - 22.2	1.18 ± .14	6.46 ± .78
WP^3	38	20.24 ± .20	16.8 - 22.5	16.3 - 24.2	1.21 ± .14	6.02 ± .69
WP^4	43	20.60 ± .18	17.3 - 22.6	16.8 - 24.4	1.18 ± .13	5.76 ± .62
WM^1	42	19.25 ± .13	16.9 - 20.8	16.5 - 22.0	.84 ± .09	4.41 ± .48
WM^2	49	19.53 ± .13	17.0 - 21.2	16.6 - 22.5	.90 ± .09	4.62 ± .46
WM^3	43	18.01 ± .12	16.2 - 19.9	15.4 - 20.6	.80 ± .09	4.47 ± .48
TCS	18	92.16 ± .99	82.2 - 97.7	78.5 - 105.8	4.22 ± .70	4.64 ± .76
LP_2	30	16.16 ± .20	13.5 - 18.7	12.6 - 19.7	1.09 ± .14	6.70 ± .87
LP_3	52	15.12 ± .11	13.5 - 16.7	12.6 - 17.7	.78 ± .08	5.15 ± .50
LP_4	61	15.00 ± .09	13.4 - 16.7	12.7 - 17.3	.72 ± .06	4.79 ± .43
LM_1	60	14.39 ± .12	12.2 - 15.9	11.3 - 17.4	.94 ± .09	6.58 ± .60
LM_2	60	14.75 ± .14	12.5 - 17.2	11.1 - 18.4	1.12 ± .10	7.62 ± .69
LM_3	48	18.45 ± .12	16.7 - 20.9	15.8 - 21.1	.81 ± .08	4.40 ± .45
WP_2	31	9.06 ± .13	7.1 - 10.3	6.7 - 11.5	.74 ± .09	8.27 ±1.04
WP_3	57	12.09 ± .09	10.3 - 13.3	9.8 - 14.4	.70 ± .07	5.79 ± .54
WP_4	59	12.78 ± .10	10.8 - 14.3	10.3 - 15.3	.78 ± .07	6.15 ± .56
WM_1	61	11.81 ± .09	10.2 - 13.2	9.6 - 14.0	.67 ± .06	5.69 ± .51
WM_2	58	11.13 ± .08	9.7 - 12.1	9.2 - 13.1	.60 ± .06	5.40 ± .50
WM_3	43	9.77 ± .08	8.5 - 10.7	8.1 - 11.4	.51 ± .05	5.24 ± .56

Table 3. Dental statistics of the total progressive population (*Parahippus barbouri*, *Parahippus leonensis*, and *Merychippus gunteri* of White).

younger age group and the total frequency distributions of crown height fails, however, to bring this expectation to realization. The distinctness of the age groups may have been obliterated due to an increase in mean height of the crown during the interval of deposition at Thomas Farm.

TABLE 4

	N	$\bar{X}$	O.R.	S.R. (S.D.)	σ
dP^2	3	.78	.78 - .79	- - - - -	- - - - -
P^2	32	.97 ± .007	.84 - 1.02	.81 - 1.07	.040 ± .005
dP^3	5	1.03 ± .011	1.00 - 1.07	.95 - 1.11	.024 ± .008
P^3	37	1.22 ± .010	1.03 - 1.34	1.02 - 1.42	.061 ± .007
dP^4	3	.99	.94 - 1.03	- - - - -	- - - - -
P^4	43	1.24 ± .011	1.05 - 1.39	1.01 - 1.47	.071 ± .008
dP_2	5	.48 ± .007	.46 - .50	.43 - .53	.015 ± .005
P_2	28	.56 ± .005	.52 - .61	.47 - .65	.029 ± .004
dP_3	6	.70 ± .008	.68 - .73	.64 - .76	.020 ± .006
P_3	47	.80 ± .006	.70 - .89	.68 - .92	.038 ± .004
dP_4	7	.66 ± .005	.64 - .67	.62 - .70	.012 ± .003
P_4	54	.85 ± .006	.73 - .98	.71 - .99	.044 ± .004

Table 4. A comparison of the width/length ratios of the deciduous and permanent premolars in the total progressive population.

A small sample of milk molars was available in the larger population. The width/length ratio is more characteristic of the deciduous set than the linear dimensions and is compared with that of the permanent dentition in Table 4. This ratio appears to be of value in the assignment of isolated teeth to the proper set. The means are distinctive with but modest overlap in the standard ranges. As is common in horses, the milk molars are both longer and narrower than their successors. The variation in the ratio is notably greater in the permanent series.

Although this investigation is concerned chiefly with measurable traits, valid species, may, of course, exhibit no significant differences in such characters and yet be separable on nonmetrical or qualitative grounds. Careful attention, therefore, was directed to the several characters which have been considered diagnostic of the four species. These include principally:

amount of cement, degree of hypsodonty, prominence of cingula, distinctness of metaconid and metastylid, development of plications (largely from the metaloph) and the degree of union of the various lophs. Detailed descriptions and figures of the proposed species were presented by Simpson (1932) and White (1942) and need not be repeated here. White emphasized the considerable variation and intergradation in these characters, which make for difficulty in species identification. Additional collecting has served to demonstrate intergradation at even more subtle levels, though the range of morphological expression remains about as previously known. The manifestation of the crochet in the total sample varies from essentially a *Miohippus* to a *Merychippus* stage, i.e., from complete absence to full union with the protoconule at an early stage of wear. Cement is absent or scantily present in the more primitive species while the larger group most often has a moderately heavy coat, though the variation is extensive. In the more progressive forms the metaloph plications may be several or almost totally wanting. The distinctness of the metaconid and metastylid, though varying in these forms, offers no opportunity for taxonomic separation. In short, detailed study of these and other traits has revealed no valid basis for distinguishing more than two populations within the total assemblage. In general, within the larger population, the linear dimensional traits and the degree of hypsodonty tend to be positively correlated with the amount of cement, complexity of the plications and the extensiveness of crest development, though the association is by no means complete.

DISCUSSION

The results of this detailed investigation substantiate the more superficial impression gained from field work, i.e., that specimens are assignable without equivocation to a larger or smaller population, but only with great difficulty (and, then, with little enough assurance) allocated to one of the described species of the larger group. *P. barbouri* was separated from *P. leonensis* primarily because of its smaller size and modest crochet development. With one exception, the specimens referred to the former are clearly small members of the latter, as evidenced by the want of an appropriate mode in the frequency distribution, the similarity in the width/length ratios as seen in the scatter dia-

grams, the failure of the inclusion of these specimens to do violence to the magnitude of the V of *P. leonensis*, and the almost perfect intergradation demonstrated by crochet development. One specimen (M.C.Z. 3742), alluded to in the previous section, is, on strictly statistical grounds, very improbably a member of the larger population. It cannot be absolutely excluded on this basis, however, and since there was probably some evolution toward larger size in the population, its separation would be even more unjustified.

The difficulty attendant upon the consistent separation of *P. leonensis* and *M. gunteri* was recognized by both Simpson and White. White (1942, p. 23) stated, "The transition between the two species is well represented by complete dentitions. Fortunately it is still possible to set up an arbitrary rule which will distinguish the conservative members of this species [*M. gunteri*] from the progressive members of the preceding one. This rule is:—The crochet must have joined the protoconule on M^{1-2} by the time wear has exposed the principal cusps on M^3 before the specimen can be placed in *M. gunteri*. At this time both species have a height of tooth at the mesostyle on M^2 of 10 mm. When the teeth of the progressive specimens of *P. leonensis* are worn so that M^2 has a height of 7.5 mm. at the mesostyle they display most of the characters of *M. gunteri*." This criterion is, admittedly, completely arbitrary and leaves many of the specimens (in the middle and later wear stages) indeterminable. It is much to be preferred to group these progressive forms with the other larger specimens for much the same reasons as indicated for *P. barbouri* (only a very small percentage have been found which satisfy White's rule). Again, no evidence of segregation within the lineage can be discerned.

It happens that individuals which are here referred to one species were placed by White not only in different species and genera but in different subfamilies (employing the arrangement of Simpson, 1945). The difference in the two viewpoints is, of course, not nearly so great as would be inferred from the alternative taxonomic schemes; rather, it is largely a reflection of the excellent documentation of horse evolution. Now, it is clear that a few of these specimens so assigned to *P. leonensis* exhibit *Merychippus* qualities and would be properly referred to that genus if found in isolation though the modal expression of the popula-

tion to which they belong remains parahippine in nature. In making taxonomic decisions the total situation must, of course, be evaluated. A specific separation of these specimens would imply that two populations (between which interbreeding was absent or minimal) coexisted at the same time and in the same general area, an hypothesis for which there is no adequate justification on the basis of the known evidence. Traits uniformly present in a species do not arise *de novo* but spread gradually throughout the population until they become fixed. A contemporaneous interbreeding assemblage, only a part of which possesses a given character or whose members vary in the degree of character expression, should not be split into different species simply because the character in question is highly diagnostic of closely related taxa. The development of the crochet is an excellent case in point. The overwhelming majority of equid genera are characterized either by complete absence of this crest or by its full union with the protoconule, the primary exceptions including a few species of *Miohippus* and *Archaeohippus* and the species of *Parahippus*. The elapsed time from its inception to ultimate expression must be in the order of 5 million years as a minimum. Thus, while it is of taxonomic importance before and after this development period, its diagnostic value during the transition is greatly reduced (although not altogether eliminated) and its arbitrary use completely unjustified. It cannot be seriously doubted that in the later stages of the time represented by the deposits at Thomas Farm, some members of an essentially contemporaneous population exhibited the typical *Parahippus* mode of crochet development while others possessed the *Merychippus* type, a not unexpected situation if the two did, indeed, have an ancestral-descendant relationship. Simpson (1944) has discussed certain theoretical implications of the incorporation of this "mutant" in equid populations.

A similar example concerns the smaller population, *P. blackbergi*. White (1942) assigned a few isolated upper teeth to *Miohippus* sp., primarily on the basis of the incomplete union of the ectoloph and metaloph. Since the dimensions of these teeth are close to the means of their homologues in the *P. blackbergi* sample, it is most probable that they are deviants of the same population, though failure of ectoloph-metaloph union, if taken at face value, would certainly exclude them from that genus. There remains the

possibility that such deviations may occasionally be due to non-heritable factors, producing essentially a phenocopy. This "lumping" procedure facilitates the study of the dynamics of evolving populations while detracting in no wise from the biological meaningfulness of a group so long as the deviants are fully discussed in the species descriptions. The inferential determination of populational characteristics, not those of individuals as such, is the proper object of taxonomic inquiry, but this is a concept too often ignored even in modern paleontological work (see Simpson 1943). It offers, however, the best hope of bringing some order out of the chaos in which taxonomic paleontology (at least in many areas) finds itself today.

There remains one other taxonomic possibility to consider, i.e., the use of subspecific names for the different phases of evolution in the larger group. This has been rejected due to the lack of detailed stratigraphic records and independent criteria with which the names might be associated, e.g., different formations or members. The dilemma posed by the vertical species (or subspecies) concept is well known. The differences in the relationships of contemporaneous as opposed to vertical populations are several and profound. From a strictly taxonomic viewpoint, increased knowledge enhances the understanding of the former while tending to reduce the latter to the absurd. Contrariwise, the untenable consequences of continued extension of vertical unit limits has been pointed out by Simpson (1932) and others. Fortunately for the present Linnean procedures in paleontology, a continuous record of the type seen at Thomas Farm is usually of limited vertical extent. *P. leonensis* (present usage) probably exhibits a somewhat greater range of variability in non-dimensional traits than any species of the genus heretofore defined. A revision of the genus would, however, almost certainly result in the placing of many names in synonymy, effecting an increase in the variation of the valid species. As indicated in the previous section, the dimensional variation is quite within the usual range.

The major outlines of the relationships of these Thomas Farm horses emerge with considerable clarity. That there were, at any one time, but two distinct, non-interbreeding populations seems reasonably certain. These two populations, though manifestly closely related, present little or no evidence of intergradation. If the smaller species is, indeed, the progenitor of the larger

(which is probable), the evidence must be sought in the deeper levels of the Thomas Farm "dig" or elsewhere in deposits of somewhat earlier age. It may be assumed that some evolutionary change occurred in both populations *in situ*, and to a greater degree in the larger population. Although detailed stratigraphic records were not kept on the earlier material collected from the site, it was noted by White (1942) that several "*species*," including *Merychippus gunteri* (in his sense) were found only in the initial phases of the excavation. Teeth falling into this category, according to White's rule, have more recently been found at deeper horizons, but are extremely rare. The dimensional means of all of these more advanced teeth are as a rule greater than those of the remainder of the population, though the difference is not statistically significant. Dimensions of teeth and posteranial elements taken in the past two years from the deepest portion of the pit (now about 20 feet below the surface) are generally below their respective means for the larger population as a whole. Simpson (1930) described *M. gunteri* from Midway, also referring several specimens from Quincy to it. The fauna from these localities is much less perfectly known than that of Thomas Farm, practically nothing having been added to our knowledge since Simpson's report. Though intergradation with the more advanced specimens of Thomas Farm is apparent, the typical development of these Midway and Quincy horses is somewhat more advanced, exhibiting essentially merychippine characters. That this group is derived from the larger population at Thomas Farm, as Simpson tentatively suggested, is now established beyond any reasonable doubt. If the interpretation presented here is correct, the absence of "*P. barbouri*" and "*P. leonensis*" from the Midway-Quincy deposits is satisfactorily explained. The occurrence of *P. blackbergi* throughout the Thomas Farm deposit and probably at Midway also (Simpson, 1932) demonstrates its coexistence, in a relatively unchanged state, with its larger, more progressive descendant. It has been found in the later Miocene of the West although not reported above the Garvin Gulley horizon in Texas. These interpretations are diagrammatically presented in Figure 6.

In these Miocene equids, factors controlling such characters as quantity of cement, hypsodonty, and complexity of the enamel pattern appear to be moving through the population at a fairly

rapid rate, undoubtedly under selective control, as the grazing niche of the plains is more fully exploited. Simpson (1944), suggested that the shift from a browsing to a grazing adaptive peak partook of characteristics which he termed quantum evolution. If such an evolutionary mode existed (its most convincing

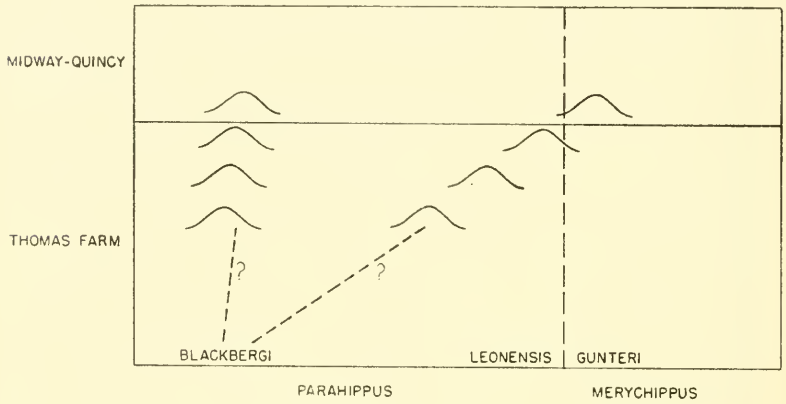


FIGURE 6

Figure 6. A schematic presentation of the relationships of the horses of Thomas Farm and Midway-Quincy, late lower and early middle Miocene respectively (see text).

support has come and, of necessity, must continue to come, from negative evidence), the larger population at Thomas Farm is in the post-quantum phase, moving fairly rapidly up the slope of the grazing adaptive peak. The smaller population remains under the influence of the selective forces for browsing. The transition between them would entail passage through the inadaptive "valley." It should be extremely interesting to see what sort of intergradation between the two, if any, is revealed by continued excavation at the "dig."

The relationships of selection, variation, population size, and rate of change are quite complex. The horse sequence at this site offers a rather limited opportunity for evaluation of these interrelationships due to the restricted time interval involved. Certain features may, however, be briefly considered. It may be

inferred that there is a strong linear component to the selection on the larger group while that on the smaller population was primarily centripetal in nature. The coefficients of variation given in Tables 2 and 3, closely similar in the two species, have a vertical as well as a horizontal component. It may be assumed with some confidence that the variation exhibited by contemporaneous populations was lower in *P. leonensis*, since it was changing at a more rapid rate. If so, the relationship of quantitative variation and evolutionary rate would appear to be similar to that shown in the oreodonts over a longer temporal interval (Bader, 1955). In the Thomas Farm horses, however, population size is positively correlated with rate of change, the opposite being true in the oreodonts.[1]

The proper Linnean designation of the two populations presents a problem. The smaller population was described as *Archaeohippus nanus* by Simpson (1932) and was referred to *Parahippus* [*Miohippus*] *blackbergi* Hay 1924 by White. Adequate comparative material has not been available during this investigation to make a meaningful choice between these two genera, the relationships of which are far from clear. However, if *Archaeohippus* represents a natural assemblage, the smaller species should be assigned to it. The valid application of the specific name *nanus* as opposed to *blackbergi* hinges on the question of conspecificity between the Florida and Texas forms. Quinn (1955 and personal communication) found little overlap in length-width measurements of small samples from the two areas. It is hoped that more extensive comparisons can be made in the near future. Pending further studies, I prefer to follow White. The larger population was included in *Parahippus* by Sellards, Simpson and White; however, Quinn (1955), in the most extensive revision of the post-Oligocene equids of the past several years, placed the previously described species of this population in *Hippodon*, a genus redefined by him after its description by Leidy in 1854 and subsequent rejection. *Parahippus*, a genus originally described from milk molars, has not been rigorously defined and may (along with *Merychippus*) represent a structural stage attained independently by several phyla, as Quinn

[1] It is assumed, in the absence of evidence to the contrary, that the sample sizes of the several species offer a reliable indication of the relative abundance of the populations in nature.

infers. However, the distinction between *Hippodon* and *Parahippus* remains nebulous and it is to be doubted whether the resurrection of the former will effect a greater understanding of the relationships of early and middle Miocene Equidae if it is merely to be substituted for the latter.[1] The problem of the correct designation of the Thomas Farm species can be solved only through a study far outside the confines of the present investigation. A revision of the entire assemblage of Miocene Equidae is clearly in order. Until such revision (a truly monumental task) is undertaken, it is preferred to tentatively retain the names used by White, *P. blackbergi* and *P. leonensis* (the oldest available name for the larger species).[2]

A sequence very similar to that in Florida is seen in the Texas Gulf Coastal Plain, species conspecific (or nearly so) with the Florida Miocene equids appearing in progressively later strata. Several possible relationships of the faunas of the two areas suggest themselves: both areas could have been populated by successive immigrations from the north; Florida may have been the principal site of evolution with repeated emigrations to Texas (or vice versa); the two populations could have evolved in parallel fashion from a common ancestry; or one continuous progressive population may have occupied the Gulf Coastal region and evolved essentially as a unit to the *Merychippus* stage, with the continued survival of the primitive *P. blackbergi,* the progenitor of the sequence. The last hypothesis is the most tenable. The intergradation, particularly in Florida, is too com-

[1] This is not the place to attempt a full review of Quinn's interesting study, though it may be noted that in some ways his approach is almost diametrically opposed to that used here; witness, for example, the recognition of seventeen contemporaneous horse species (and eleven genera) in the latest upper Miocene (LaPara Creek) from a limited area of the Texas Gulf Coastal Plain. Quinn correctly points out that application of the Gause principle must be made with caution when dealing with a thanatocoenose rather than a biocoenose. This does not imply, however, that the principle may be completely ignored or that it may not judiciously be applied at an order of magnitude level, particularly when dealing with a restricted time interval. A situation even remotely approaching that depicted for these Texas forms is an extreme rarity among the larger modern mammals. On the other hand, Quinn has properly stressed the importance of the lower teeth, heretofore largely ignored in classificatory studies.

[2] Mr. Bryan Patterson has pointed out that the smaller species, when compared with the larger form, has longer lateral metapodials relative to the median metapodials, more slender proximal phalanges and a somewhat different incidence of the various ligamentary scars. These pedal disparities, in addition to the differences in the dentitions, are cogent reasons for placing the forms in different genera. However, the problem of the correct generic assignation remains, as outlined above.

plete to invoke an immigration hypothesis. Parallel evolution is possible, though rendered improbable by the great similarity of the two series. Whether there occurred but one progressive population at any one time is, of course, difficult to demonstrate. The hiatus in material from the area between Texas and Florida, is complete and likely to remain so. A more intensive comparison of the terminal members of the distribution (Texas and Florida) should aid in the interpretation. Quinn's suggestion (1955) that the Garvin Gulley is slightly older than the Thomas Farm was based on the relationship of the equids and certain other genera, such as *Synthetoceras*. This has not been definitely established but may be true and is tentatively accepted here pending more detailed comparisons. The relation of the two sections and their included horse faunas as now known is presented in Table 5 (based on Simpson, 1930, 1932; White, 1942; Stenzel, Turner and Hesse, 1944; Quinn, 1955; and the present study. The horse terminology is my own).

GEOLOGICAL PROBLEMS

Several problems of a geological nature have been posed by the "dig," most of which are but incompletely solved. Simpson (1932) suggested that the materials were deposited in a sink hole, a common feature in this part of Florida; White (1942) considered the lack of sorting of the material in the boulder bar and the lenticular nature of the clays to be indicative of stream action. Cooke (1945) supported the sink hole hypothesis, pointing out that the tremendous accumulation of bone demands some sort of catchment basin such as would be provided by a sink. Although articulated skeletons have not been found, a gentle water action is indicated by the unworn state of most of the material and the intact condition of some delicate structures (e.g., the mandibular coronoid process of the small cervids and the distal end of the horse ulna). Recently an articulated calcaneum and astragalus of a rhinoceros were found by S. J. Olsen and a few other articulated elements are known. W. Auffenberg (personal communication) has pointed out the similarity of the deposits at the "dig" and those in recent sinks. Intensive screening of material by Auffenberg has revealed but a single fish spine, whereas such spines occur in some quantity in most of the

TABLE 5.

Texas Section	Species	Florida Section	Species	Marine Formation
Burkeville	*Merychippus gunteri*	Midway-Quincy	*Merychippus gunteri* *Parahippus blackbergi*	Hawthorne
Garvin Gulley	*Parahippus vellicans* *Parahippus blackbergi*	Thomas Farm	*Parahippus leonensis* *Parahippus blackbergi*	Tampa

Table 5. The Florida and southeastern Texas terrestrial Miocene sections, their included horse faunas and their correlation with the marine formations of Florida. Only the equids considered in this study are included.

undoubted stream deposits he has worked. E. C. Pirkle has suggested the possibility that the boulder bar may be the remnant of a solution joint in the Ocala limestone, both of which trend NW-SE. It may be doubted that a stream on this low-lying land mass would be rejuvenated to an extent sufficient to transport the large boulders of the boulder bar, as proposed by White. Although incontestable evidence is yet to be forthcoming, the facts seem best accommodated by the sink theory. The alternatives are not necessarily mutually exclusive; the sink may have been fed by small streams, as are existing sinks in the area today. The mode of deposition has obvious biological implications. Since the material accumulated in a sink is usually from a more circumscribed area than that in a stream bed, the number of niches "sampled" would be smaller, and, in consequence, the number of closely related species to be expected in the deposit would be reduced.

White stated that Florida was an island at this time; Cooke (1945) suggested a narrow peninsula. Vernon (1951), while discussing other aspects of the deposit, did not choose between the alternatives. The critical evidence lies in the Okefenokee trough area to the north and appears, at present, to be inconclusive. The great similarity of the Texas and Florida horses as well as that of many other components of the two faunas indicates that the isolation of Florida must have been, at best, very ephemeral. White pictures the horses trapped on the island, from which they finally emigrated in the early middle Miocene, giving rise to the later, more advanced species of *Merychippus* in the West. That *Merychippus* has a polyphyletic origin has been advocated by several authors (e.g., Simpson, 1932, and Stirton, 1940); if this view is correct, the western development of the genus may have been relatively independent of that in Florida.

The time interval represented at the Thomas Farm was placed by White between the deposition of the Suwannee Limestone (upper Oligocene) and the Hawthorne formation (middle Miocene). Invertebrates derived from the Suwannee have been identified in the deposit; that this is the lower limit seems adequately established. Romer (1948), quoting Simpson (1932), indicated that the site was post-Tampan since the echinoid, *Cassidulus gouldii*, found here, was confined in Florida to the Tampa Limestone. The species is, however, characteristic of the Suwannee

as now recognized (Cooke and Mansfield, 1936). The surface sand and a superficial sandstone layer were identified by White, on strictly lithological grounds, as belonging to or derived from the Hawthorne. It was, therefore, assumed that the encroachment of this sea concluded the period of fresh water deposition. Vernon (1951), in a detailed study of Levy and Citrus counties (adjoining Gilchrist County), concluded that neither the Tampa nor Hawthorne seas covered the area in question, both being limited to the flanks of the Ocala uplift. He failed to recognize Hawthorne deposits within about 25 miles of the "dig," evidently rejecting White's interpretation of the sands. The Thomas Farm deposit was assigned by Vernon to the Alachua formation, the terrestrial facies of the Tampa and Hawthorne formations, and it was further suggested that the site included deposits spanning the entire Miocene. If the Hawthorne is not present, the definitive upper limit of the interval of deposition is removed. There is no paleontological reason to believe, however, that the fauna extends beyond the early middle Miocene at the latest. The fauna as a whole is best assigned to the late lower Miocene as emphasized by both White (1942) and Romer (1948). The previous allocation to the lower Miocene caused some concern since *Merychippus* first occurs in the Great Plains area in the Hemingfordian. The removal of *Merychippus* from the species list, while not altering the morphological situation, does lend greater emphasis to the late lower Miocene age of the deposit.

DENTAL CORRELATION

The most comprehensive investigation of dental correlations in mammals is to be found in the interesting and important work of Kurten (1953). The following salient facts were brought out in Kurten's study: the r value of the linear dimensions of the various members of a dental series is negatively correlated with the distance between them (the rule of neighborhood of Karl Pearson); the correlation is higher between occluding teeth than between adjacent teeth and is very similar in a given area of the dentition indicating identity of the morphogenetic "fields" in both jaws; the correlation between the terminal members of a series is often greater than expected from the rule of neighborhood, suggesting a recurvature of the field on itself;

and the correlation between functional homologous right and left teeth is very high, considerably lower where non-functional.

Coefficients of correlation (r) for dental width were calculated for both species and are presented in Table 6. Lengths were not included since the effect of wear, even though modest, would add still another variable to an already complex situation and since the labor of calculating from incommensurate sample sizes is considerable. The correlations of the lengths of the uppers in *P. blackbergi* were, however, calculated and found, in essence,

TABLE 6

(a)

	N = 9 to 14						N = 8 to 19				
	P^3	P^4	M^1	M^2	M^3		P_3	P_4	M_1	M_2	M_3
P^2	.79	.87	.67	(.45)	(.51)	P_2	.77	.85	(.47)	(.52)	.79
P^3		.95	.68	.72	(.52)	P_3		.91	.73	.68	.67
P^4			.81	.71	(.48)	P_4			.79	.77	.82
M^1				.59	(.17)	M_1				.89	.68
M^2					.76	M_2					.79

(b)

	N = 25 to 38						N = 18 to 48				
	P^3	P^4	M^1	M^2	M^3		P_3	P_4	M_1	M_2	M_3
P^2	.89	.93	.77	.71	.75	P_2	.79	.81	.82	.73	.76
P^3		.97	.87	.78	.78	P_3		.94	.84	.84	.78
P^4			.88	.81	.82	P_4			.90	.92	.82
M^1				.92	.80	M_1				.92	.69
M^2					.80	M_2					.77

Table 6. The coefficients of correlation of tooth width in *P. blackbergi* (a) and *P. leonensis*, present usage (b). Figures in parentheses are not significant. All correlations are positive.

to follow the same pattern as that of the widths. Some of Kurten's generalizations are substantiated by the present study (he did not include data from horses). In general, the rule of neighborhood is confirmed, though not without exceptions. The correlation of $P\frac{2}{2}$ and $P\frac{4}{4}$ is invariably higher than that of the former with $P\frac{3}{3}$. The correlation of the last molar follows almost a random pattern, being greatest with the last premolar in three of the four examples. The low correlations of M^3 in *P. blackbergi* may be spurious due to the small sample. There is some tendency for the correlation of the third molar with more anterior members of the series to be greater than that of the second molar with the same members but this is not as striking

as in some of Kurten's data which led him to suggest a recurvature of the field. The disparity in correlations between the two species is, for the most part, insignificant.

Although the dental battery has been considered a highly integrated complex by most students of fossil and Recent mammals, correlations within this series are usually lower than those between the different skull elements or between various postcranial structures (Olson and Miller, 1951, and unpublished data). The nature of the morphogenetic field is, as stressed by Kurten and previous workers, certainly very complex. In dental traits as with other quantitative, polygenic characters there remains the strong possibility that the character selected for study, e.g., width of tooth, is not a manifestation of the primary action of any genetic determinant but rather a secondary result or "by-product" of the action of a very large number of determinants. Although there is a pressing need for some understanding of the heredity of the dental and osteological characters commonly employed by the paleontologist, solutions to problems in this area will not be readily available in the foreseeable future.

ACKNOWLEDGMENT

I would like to acknowledge my indebtedness to Dr. A. S. Romer, Museum of Comparative Zoology, Harvard University, and to Dr. Herman Gunter, Florida State Geological Survey, for generously loaning material in their care for study. One specimen was borrowed from the U. S. National Museum, Washington, D. C. Although my interpretation of the facts is somewhat at variance with those of Dr. Theodore E. White, I am deeply indebted to his earlier studies of the fauna. The many courtesies extended by Mr. Stanley J. Olsen, Florida State Geological Survey, were greatly appreciated. Funds for field work were supplied by the Department of Biology and the Florida State Museum, University of Florida. Thanks are due to Dr. E. C. Olson and Dr. R. G. Johnson, University of Chicago, for making space and equipment available during the course of this investigation. Mr. Bryan Patterson, Museum of Comparative Zoology, Harvard University, critically examined the manuscript and suggested several changes which were incorporated in the text; however, I am solely responsible for the opinions expressed herein.

LITERATURE CITED

AUFFENBERG, W.

1956. Remarks on some Miocene anurans from Florida, with a description of a new species of *Hyla*. Breviora, No. **52**: 1-11.

BADER, R. S.

1955. Variability and evolutionary rate in the oreodonts. Evolution, **9**: 119-140.

BRODKORB, P.

1954. A chachalaca from the Miocene of Florida. Wilson Bulletin, **66**: 180-183.

COOKE, C. W.

1945. Geology of Florida. Bull. Florida Geol. Surv., **29**: 1-339.

——— and W. C. MANSFIELD

1936. Suwannee limestone of Florida (abstract). Proc. Geol. Soc. Amer., (1935): 71-72.

GOIN, C. J. and W. AUFFENBERG

1955. The fossil salamanders of the Family Sirenidae. Bull. Mus. Comp. Zool., **113**: 497-514.

KURTEN, B.

1953. On the variation and population dynamics of fossil and recent mammal populations. Acta Zool. Fennica, **76**: 1-122.

MATTHEW, W. D.

1924. Third contribution to the Snake Creek fauna. Bull. Amer. Mus. Nat. Hist., **50**: 59-210.

OLSON, E. C. and R. L. MILLER

1951. A mathematical model applied to a study of the evolution of a species. Evolution, **5**: 325-338.

QUINN, J. H.

1955. Miocene Equidae of the Texas Gulf Costal Plain. Bur. of Econ. Geol. Univ. Texas, Publ. **5516**: 1-102.

ROMER, A. S.

1948. The fossil mammals of Thomas Farm, Gilchrist County, Florida. Jour. Florida Acad. Sci., **10**: 1-11.

SELLARDS, E. H.

1916. Fossil vertebrates from Florida: a new Miocene fauna; new Pliocene species; the Pleistocene fauna. Ann. Rep. Florida State Geol. Surv., **8**: 77-119.

SIMPSON, G. G.

1930. Tertiary land mammals of Florida. Bull. Amer. Mus. Nat. Hist., **59:** 149-211.

1932. Miocene land mammals from Florida. Bull. Florida Geol. Surv., **10:** 7-41.

1943. Criteria for genera, species and subspecies in zoology and paleontology. Ann. New York Acad. Sci., **44:** 145-178.

1944. Tempo and mode in evolution. Columbia University Press, New York.

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85:** 1-350.

STENZEL, H. B., F. E. TURNER, and C. J. HESSE

1944. Brackish and non-marine Miocene in southeastern Texas. Bull. Amer. Assoc. Petrol. Geol., **28:** 977-1011.

STIRTON, R. A.

1940. Phylogeny of North American Equidae. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **25:** 165-198.

TIHEN, S. A.

1951. Anuran remains from the Miocene of Florida, with the description of a new species of *Bufo*. Copeia (3): 230-235.

VANZOLINI, P. E.

1952. Fossil snakes and lizards from the lower Miocene of Florida. Jour. Paleont., **26:** 452-457.

VERNON, R. O.

1951. Geology of Citrus and Levy Counties, Florida. Bull. Florida Geol. Surv., **33:** 1-256.

WHITE, T. E.

1942. The lower Miocene mammal fauna of Florida. Bull. Mus. Comp. Zool., **92:** 1-49.

WILLIAMS, E. E.

1953. A new fossil tortoise from the Thomas Farm Miocene of Florida. Bull. Mus. Comp. Zool., **107:** 537-554.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 3

ANEURETUS SIMONI EMERY, A MAJOR LINK IN ANT EVOLUTION

by E. O. Wilson, T. Eisner, G. C. Wheeler and J. Wheeler

With Three Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
August, 1956

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY

AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 115.

Breviora (octavo) 1952 — No. 57 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899-1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 3

ANEURETUS SIMONI EMERY, A MAJOR LINK IN ANT EVOLUTION

by E. O. Wilson, T. Eisner, G. C. Wheeler and J. Wheeler

With Three Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
August, 1956

No. 3 — ANEURETUS SIMONI *Emery, a Major Link in Ant Evolution*

By E. O. WILSON,[1] T. EISNER,[1] G. C. WHEELER,[2] and J. WHEELER[2]

INTRODUCTION

To students of ants, the genera of the tribe Aneuretini (*Aneuretus, Protaneuretus, Paraneuretus,* and *Mianeuretus*) have always been of primary interest because of their supposed intermediate phylogenetic position between the most primitive known ants (Myrmeciinae, Ponerinae) and the advanced subfamily Dolichoderinae. Few tribes of ants have been more deserving of careful study, and yet few have been so little known or so inaccessible to myrmecologists. *Aneuretus simoni*,[3] the only living species of the tribe, is known only from Ceylon and has been reported from only three collections made there. Until recently the total number of specimens in the museums of the world numbered no more than five or six. Published descriptions have contained only sketches of the gross features of external morphology, and no information whatsoever has been available concerning the internal anatomy, ecology, or behavior of this ant.

During a recent visit to Ceylon one of us (Wilson) made a special attempt to find *Aneuretus simoni* and study it in the field. This attempt was successful to an unexpected degree. Not only were large series of *A. simoni* collected, including all brood stages and adult castes, but a strong beginning was made in the study of the ecology and behavior of the species. Upon his return to the United States in September, 1955, Wilson turned over part of his collection of *Aneuretus* to the Wheelers, who are currently engaged in comparative anatomical studies of ant larvae, and to Eisner, who at that time was in the process of completing a comparative anatomical study of the ant proventriculus. The present paper is the product of the cooperative effort of the four authors, each of whom has concentrated on

[1] Biological Laboratories, Harvard University, Cambridge, Mass.
[2] Department of Biology, University of North Dakota, Grand Forks, N. D.

[3] Equals *Aneuretus butteli* Forel, 1913, Zool. Jahrb. (Abt. Syst.), *36:* 87, fig. A1, queen, *NEW SYNONYMY*. This species was based on an isolated queen, which we have now definitely associated with the *A. simoni* worker. Types of both species have been recently examined by Wilson in the Museum d'Histoire Naturelle, Geneva.

those aspects of special interest to himself. Specifically, Eisner and Wilson have collaborated in the section on adult morphology, the Wheelers have contributed the section on larval morphology, and Wilson has contributed the sections on distribution, ecology, and phylogeny.

ADULT MORPHOLOGY

Worker. (Pl. 1, figs. E, F, H, I; Pl. 2, fig. B; text-figs. 1, 2). A surprising discovery, made when the first nests of *Aneuretus simoni* were opened, was that the worker caste of this species is dimorphic. As shown in the size-frequency histogram of Figure 1, this is true *complete* dimorphism, with intermediates lacking. While the distribution given represents only a single colony, it is probable that if all the colonies collected were compounded, two completely discrete size-distributions would still be obtained. As shown in Plate 1, the major worker differs from the minor primarily in its proportionately larger and broader head, and in its relatively shorter, stouter propodeal spines. In the queen, it will be noted, both of these allometric trends are carried a bit further. The head is wider with respect to its length than in the worker castes, and the propodeal spines are reduced to mere angles.

The following description is based on the minor worker. Eyes small, containing only about 30 ommatidia. Antennae 12-segmented, with the segments of the flagellum increasing distally both in length and width. Clypeus broad and flat, lacking a median carina, the anterior border strongly emarginate in full-face view. Mandible as shown in Plate 2*B*. Mandibular dentition reminiscent of *Dolichoderus* (*s. str.*), relatively constant except in the following two characters: (1) the shapes of all the individual teeth vary somewhat, and (2) the number of the reduced median teeth (located between the three apical and three major basal teeth) varies from four to eight. Maxillary palp 3-segmented, the terminal segment showing a variable median constriction or local cuticular thickening, which may well indicate a phylogenetically recent fusion site. Labial palp 4-segmented.

Alitrunk as figured. Propodeal spines spike-like, tapering abruptly near the tips to form sharp points; seen from above,

they diverge from one another strongly. Metasternal gland bulla prominent, its openings supplied with a small number of coarse guard hairs originating from both the dorsal and ventral lips.

Anterior peduncle of petiole long and slender, somewhat narrowed toward its anterior attachment. The petiolar node well differentiated from the anterior peduncle by dorsal and lateral swellings. Seen from above, the node proper is nearly twice as broad as long. Posteriorly, it narrows abruptly to the point of attachment to the gaster.

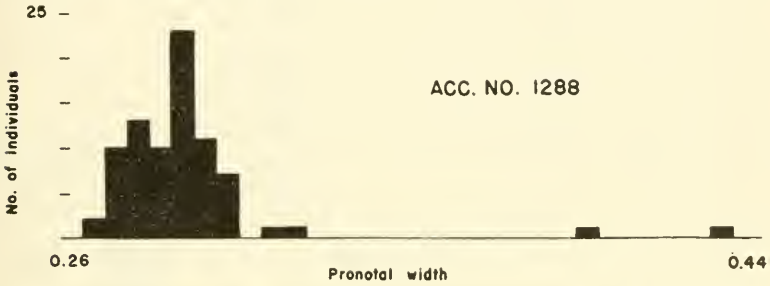


Fig. 1. Size-frequency histogram of the entire worker population of a single colony of *Aneuretus simoni* from Ratnapura, Ceylon, showing worker dimorphism.

The gaster lacks any form of intersegmental constriction whatsoever. The sting is well-developed, sclerotized, and exsertile.

Integument relatively thin and collapsible, resembling in this respect that of the higher dolichoderines and formicines. Color of living and fresh alcoholic material varies within most nest series from light yellow (in callows) to medium yellowish orange. Body lightly shagreened overall, subopaque to feebly shining; the dorsal and most of the lateral surfaces of the propodeum are in addition transversely rugulose.

Pilosity generally sparse. Appendages covered with abundant short, oblique pubescence, but lacking longer hairs except on the coxae and tarsal claws. Body supplied with scattered, relatively long, pointed erect hairs distributed as shown in Plate 1; body pubescence appressed and sparse.

Proventriculus as shown in Text-figure 2. Because of its extremely small size and flaccid framework this organ is easily deformed during preparatory handling, and it accordingly varies

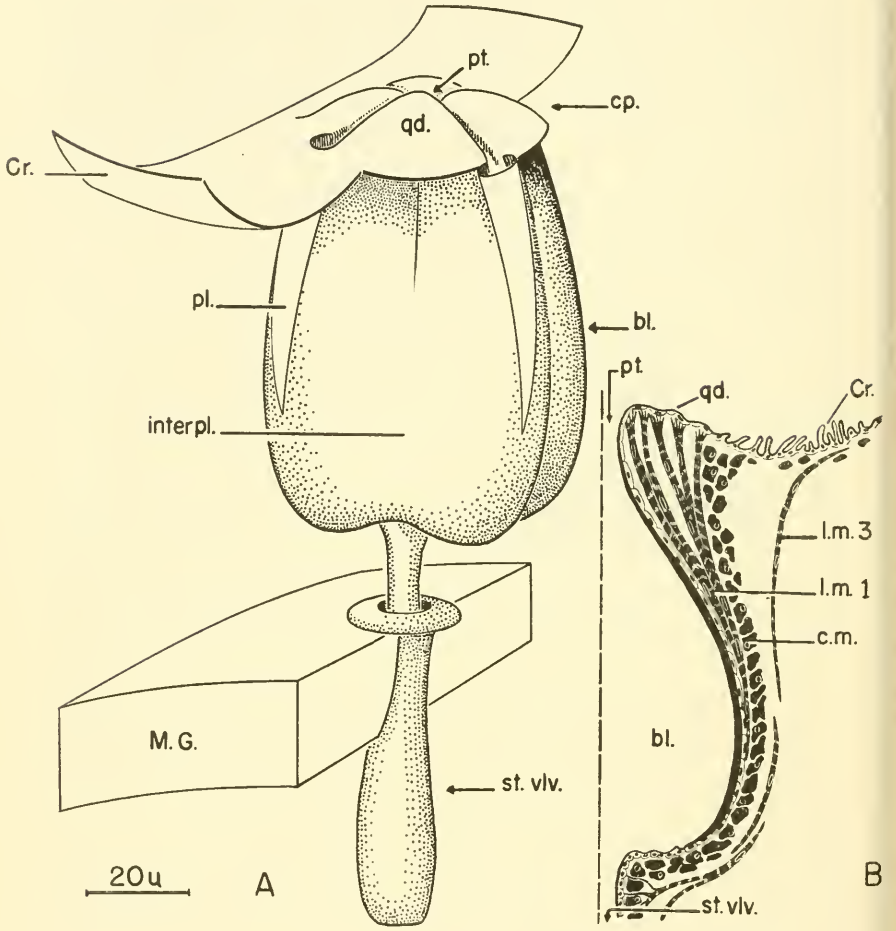


Fig. 2. Worker proventriculus of *Aneuretus simoni*. *A*, cuticular framework with musculature removed. *B*, longitudinal section through interplicary plate and portal quadrant, showing musculature. *Bl.*, bulb; *c. m.*, circular muscles; *cp.*, cupola; *Cr.*, crop; *interpl.*, interplicary plate; *l. m.* 1 and *l. m.* 3, longitudinal muscles; *M. G.*, midgut; *pl.*, plica; *pt.*, portal; *qd.*, cupolar quadrant; *st. vlr.*, stomadaeal valve. Further explanation in the text.

from one preparation to the next; for this reason, the habitus portrayal of Text-figure 2 must be considered semidiagrammatic. The terminology of the following description is the same as that adopted in the forthcoming monograph on the formicid proventriculus by Eisner. The cuticular framework consists of a thin-walled, flask-shaped bulb (*bl.*), opening anteriorly into the crop (*Cr.*) through a relatively wide cruciform portal (*pt.*). The walls of the bulb are four broad, sclerotized, inwardly curved interplicary plates (*interpl.*), joined basally and merging into a slender, tubular stomodaeal valve (*st. vlv.*). The thin and flexible cuticle of the valve, after extending into the midgut, folds back upon itself so as to constitute a compound tube. The interplicary plates of the bulb are separated from one another by relatively narrow longitudinal strips of thin, flexible cuticle, the pleats or plicae (*pl.*), and extend anteriorly into the lumen of the crop as four apically rounded lobes or quadrants (*qd.*), which collectively constitute the cupola (*cp.*). Actually, the cruciform shape of the portal is determined by the presence of the cupolar quadrants. The bulb is surrounded by a strongly developed layer of circular muscles (*cm*, Text-fig. 2B). The longitudinal muscles are arranged in two distinct groups (*l. m.* 1 and *l. m.* 3). The more strongly developed of these muscles (*l. m.* 1) originate on the interplicary plates of the bulb, extend over the plates and insert anteriorly on the quadrants of the cupola. The second group (*l. m.* 3) consists of a few scattered fibers that extend from the crop to the midgut outside the circular muscles. Some of these fibers terminate at the base of the proventriculus, where they insert on the cuticle at the point of origin of the stomodaeal valve.

The glandular system has not yet been studied, but it is noteworthy that in the field the workers defending their nests were never observed to produce anal droplets, nor did they produce the "Tapinoma-odor," resembling rancid butter or coconuts, which is supposed to characterize most Dolichoderinae.

Queen. (Plate 1.) The queen is much larger in size than either of the worker subcastes and differs further in its proportionately broader head and greatly reduced propodeal spines. In addition, it is much darker, being overall dark brown. It is essentially similar to the workers in petiolar structure, mandibular dentition, pilosity, sculpturing, etc.

The wing venation (of both the queen and the male) is relatively generalized and similar to that of the most generalized true dolichoderine, *Dolichoderus s. str.*, as typified by *D. attelaboides* (Fabr.). The latter species, as pointed out by Brown and Nutting (1950) in their important review of formicid wing venation, possesses all of the venational elements of the primitive ponerine pattern except for the first radial cross-vein. *Aneuretus simoni* shows two significant further advances. First, Mf2 is completely contracted, so that the ends of Rs2 and the cross-vein

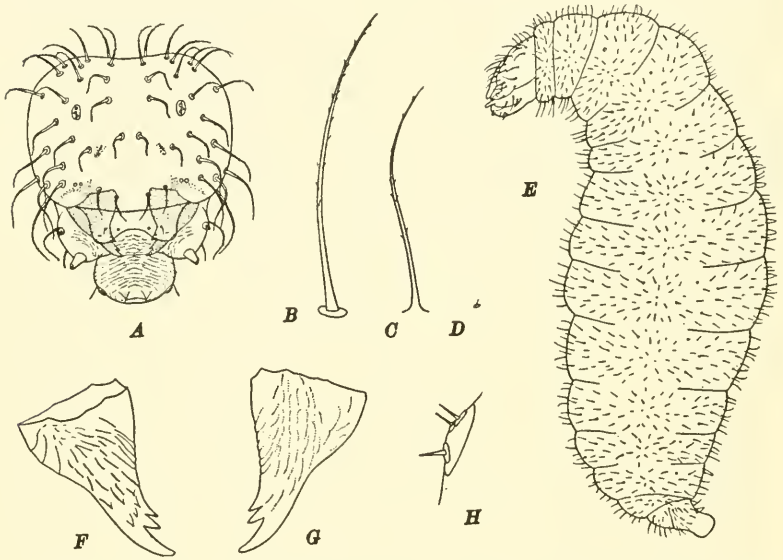


Fig. 3. Larva of *Aneuretus simoni* (immature). *A*, head in anterior view, X 130. *B-D*, three types of body hairs, X 546. *E*, larva in side view, X 43. *F*, left mandible in posterior view, X 325. *G*, left mandible in anterior view, X 325. *H*, left antenna in lateral view, X 546.

m-cu are contiguous. Second, Rs4 has contracted to bring about the alignment of the cross-veins 2r and r-m.

Male. Plates 1 and 2 show almost all of the important features of external morphology of this caste. Especially noteworthy are the conservation of the "myrmecioid" petiolar structure shown also by the worker and queen, the relatively generalized structure

of the mandible, and the generalized structure of the genitalia, especially the volsella. One perhaps significant advanced feature is the absence of serration on the ventral edge of the penis valve.

LARVAL MORPHOLOGY

Immature larva. (Text-fig. 3.) Body length (through spiracles) 1.1-2.1 mm. Straight length 0.8-1.6 mm. Somewhat sigmoidal in side view; thorax forming a stout neck which is bent ventrally at 90°; abdomen rather stout, diameter greatest at abdominal somite IV; abdominal somites IX and X small and directed posterodorsally, the tenth forming a terminal naked knob. Anus posterior. Leg and wing rudiments present. Spiracles small, decreasing in diameter posteriorly. No spinules seen on the integument. Body hairs short, moderately numerous, uniformly distributed, of three types: (1) 0.027-0.045 mm. long, slightly curved or flexuous, with a few minute denticles, without alveolus and articular membrane, the most numerous type; (2) 0.045-0.072 mm. long, longest and most numerous anteriorly, slightly curved or flexuous, with a few minute denticles, with alveolus and articular membrane; (3) minute (about 0.001 mm. long), few, widely scattered. Head moderately large, feebly cordate; cranium transversely subelliptical, with the occipital border impressed and the corners rounded. Mouth parts large. Antennae small, each with three sensilla, each of which bears a moderately long spinule. Head hairs moderately numerous, uniformly distributed, slightly curved or flexuous, long (0.027-0.072 mm.), with numerous minute denticles on the distal 2/3. Labrum short and broad (breadth 2.8 times the length), bilobed due to a rather deep impression of the ventral border; anterior surface of each lobe with one minute hair and three sensilla; ventral border with two sensilla near the middle and with a few minute spinules; posterior surface of each lobe with one large and three minute sensilla; posterior surface spinulose, the spinules minute and in numerous short arcuate rows, the rows radiating from each dorsolateral corner. Mandibles moderately large, heavily sclerotized and subtriangular in anterior view, longer than broad; slightly curved posteriorly; apex forming a rather long tooth which is slightly curved medially, two rather large subapical teeth on the medial border; anterior surface

with numerous short longitudinal ridges (rows of exceedingly minute spinules?); posterior surface with several acute denticles on the distal half and numerous ridges on the basal half, some of the ridges bearing a row of minute spinules. Maxillae lobose, with the apex a small conoid directed medially, with minute spinules in short rows which are arranged in longer rows encircling the galea; palp a frustum bearing four apical (two encapsulated and two with a spinule each) and one lateral (with a spinule) sensilla; galea a tall peg with two apical sensilla. Labium hemispheroidal and protruding; with all surfaces spinulose; the spinules more numerous and in more numerous rows on the anterior surface, and larger, fewer, and in short rows or isolated on the posterior surface; palp a slight elevation with five sensilla, three encapsulated and two bearing a spinule each. Opening of sericteries wide and salient. Hypopharynx spinulose, the spinules so long that those in adjacent rows overlap; the rows numerous and radiating from each dorsolateral angle.

The larva of *Aneuretus* shows only one dolichoderine character —— the short, broad labrum —— and even this is not distinctive. The one and only character that affiliates it with the Dolichoderinae is, strangely enough, one which is not characteristic of the subfamily at all, namely the terminal knob projecting posteriorly or posterodorsally. Now, a terminal knob occurs in the larvae of several genera in other subfamilies, but there it projects posteroventrally, ventrally, or anteroventrally. Only in the most advanced dolichoderine genera *Engramma, Tapinoma* and *Technomyrmex* have we previously found it projecting posteriorly or posterodorsally. (See G. C. and J. Wheeler, 1951.)

In marked contrast are the many non-dolichoderine characters of *Aneuretus* larvae. These are given in the accompanying table. It will be seen that all the non-dolichoderine characters of *Aneuretus* except 3 and 4 are more generalized than their dolichoderine counterparts. Thus we find *Aneuretus* standing out conspicuously as a generalized ant larva when considered in reference to the Dolichoderinae.

TABLE

Larval Characters of the Subfamily Dolichoderinae	Non-dolichoderine Larval Characters of *Aneuretus*
1. No neck	1. Neck present
2. Body and head usually almost naked, hairs typically very few and widely scattered	2. Body and head hairs moderately numerous and uniformly distributed
3. Hairs of only one type (one exception)	3. Hairs of three types
4. Hairs simple (one exception)	4. Hairs denticulate
5. Mouth parts small, spinules sparse or lacking	5. Mouth parts moderately large, with moderately abundant spinules
6. Mandibles small (ratio of head width to mandible length ranges between 4 and 10)	6. Mandibles moderately large (head width divided by mandible length=2.6)
7. Mandibles feebly sclerotized	7. Mandibles heavily sclerotized
8. Mandibles with the basal portion inflated; distal portion slender, acuminate	8. Mandibles subtriangular in anterior view (not divided into two distinct portions)
9. Mandibles without teeth on the medial border (rarely with a single small tooth)	9. Mandibles with two rather large subapical teeth on the medial border
10. Maxillary palp and galea represented by clusters of sensilla; never paxilliform	10. Maxillary palp and galea paxilliform
11. Opening of scrieteries small and inconspicuous	11. Opening of scrieteries wide and salient.

PHYLOGENETIC POSITION AND TAXONOMIC STATUS OF THE ANEURETINES

Like so many archetypal or annectant forms, *Aneuretus simoni* by itself shows a remarkable mixture of primitive and specialized characters. In some of these characters the species seems to have remained close to the mainstream of dolichoderine evolution; in others, it has moved off on a branch of its own. Before commenting on the totality of *Aneuretus* morphology and attempting to place the genus phylogenetically, let us review briefly the principal aneuretine characters and attempt to assess them with respect to their evolutionary significance.

Female mandibular dentition. In the form and placement of the basal teeth, *Aneuretus* closely resembles the primitive true dolichoderines, especially *Dolichoderus s. str.* At the same time, the set of reduced, semicircular median teeth represents a specialization not shared with any of the living dolichoderines.

Integument. The adult integument is relatively thin and collapsible, as in the higher dolichoderines and formicines.

Clypeus. In shape and proportionate size, the clypeus resembles the Dolichoderinae-Formicinae more closely than the Myrmeciinae-Ponerinae. The prominently emarginate anterior border is highly characteristic of the Dolichoderinae.

Palpal segmentation. The reduction of the number of segments in the maxillary palp is a specialization peculiar to *Aneuretus;* it is not shared by *Protaneuretus* or any primitive dolichoderine or formicine genus.

Petiole structure. The *Aneuretus* petiole, with its long anterior peduncle and low, rounded node, is undoubtedly of a very primitive type. It is in fact most similar to that of *Nothomyrmecia*, probably the most primitive of all the known living ant genera. There is nothing comparable to it anywhere in the Dolichoderinae or Formicinae.

Gaster. The absence of any constriction behind the postpetiolar segment constitutes an important difference from most unspecialized Ponerinae, and makes it unlikely that the aneuretines could have been derived from any of the known ponerine tribes. *Nothomyrmecia*, on the other hand, also lacks any form of gastric constriction.

Sting. The well-developed, exsertile sting of *Aneuretus* is a primitive character not shared by any of the Dolichoderinae or Formicinae.

Wing venation. In this character, *Aneuretus* is generalized with respect to the Dolichoderinae and Formicinae as a whole, but is more advanced than *Dolichoderus*, having undergone reductions in two important venational elements (Mf2, Rs4).

Male genitalia. Until a much-needed survey of formicid male genitalia is available, the most that can be said about *Aneuretus* is that it is unspecialized, having undergone no important reductions or modifications beyond the loss of serration on the ventral penial valve blades. By contrast, some of the higher dolichoderines have undergone such changes as partial reduction of the volsellae and complete loss of the pygostyles.

Proventriculus. The proventriculus of *Aneuretus simoni* conforms closely to the primitive formicid type, as seen in the Myrmeciinae, Pseudomyrmicinae, Ponerinae, and Cerapachyinae, which in turn does not differ much from the generalized aculeate pattern. Specifically, there is a mobile portal associated with flexible plicae in the bulb, with no suggestion of the portal growth and reinforcement through plical sclerotization seen in the higher Dolichoderinae and Formicinae. At the same time, there is apparently lacking in *Aneuretus* a group of longitudinal muscles (*l. m.* 2) which is characteristic of the lower ant groups. This lack of *l. m.* 2 is surprising in view of the otherwise primitive structure of the *Aneuretus* proventriculus, and may represent an important evolutionary step toward the proventricular type of the higher Dolichoderinae and Formicinae.

Odor. It was established in the field that *Aneuretus simoni* adults lack the "*Tapinoma-odor*" which is supposed to characterize the Dolichoderinae.

Larval morphology. The larva of *Aneuretus simoni* has only one character that definitely affiliates it with the Dolichoderinae: the posterodorsally projecting terminal knob, which is characteristic only of several of the most specialized dolichoderine genera. Otherwise, larval morphology is so generalized as to set *Aneuretus* off from the Dolichoderinae as a group. Phylogenetically the larva could have been derived from that of the Myrmeciinae, but so could the larvae of most other primitive ant groups. More immediately, it can be linked to the larvae of the more primitive

formicine genera such as *Melophorus,* which it resembles in number and shape of body and head hairs, size of mouth parts, shape and sclerotization of mandibles, and size and shape of maxillary palp and galea. *Melophorus* in turn resembles very closely the larvae of some of the Ponerinae, especially *Ectatomma* (see Wheeler and Wheeler, 1953). At the present time, however, the interrelationships of these last two genera are poorly understood, and it is not known to what extent larval morphology by itself can be used as a phylogenetic standard.

Summing up the above information, it is clear that the aneuretines, as exemplified by *Aneurctus simoni,* are a group of paramount significance in the evolution of the ants. Their relationship to the Dolichoderinae is undeniable. Some characters in both adult and larval morphology are shared exclusively with the Dolichoderinae. But in other characters, the aneuretines are so generalized as to seem to place them closer to the Myrmeciinae and Ponerinae than to the Dolichoderinae. There is evidence to suggest, and apparently none to deny, that the aneuretines represent the direct ancestors of the Dolichoderinae, and perhaps also of the Formicinae. At the same time it appears, on the important basis of external abdominal anatomy, that the aneuretines are more closely related to *Nothomyrmecia,* the living "archetypal" myrmeciine ant of Australia, than to any other primitive ant group. On the basis of these two major considerations, future phylogenists may feel justified in deriving the Dolichoderinae and Formicinae ultimately from a *Nothomyrmecia*-like stock through the aneuretines.

In the past, the aneuretines have been conventionally considered a tribe of the Dolichoderinae. The totality of anatomical evidence we have presented in this paper should now make it clear that such a taxonomic placement is awkward, since an inclusion of the aneuretines in the Dolichoderinae would make that subfamily heterogeneous out of all proportion to the remainder of the ant subfamilies, and its diagnosis would then have to depend on relatively minor characters in cephalic structure. We consider that the best course is to elevate the aneuretines to subfamily rank, coordinate with the Dolichoderinae.

Subfamily ANEURETINAE Emery

Aneuretini Emery (tribe), 1912, Gen. Ins., 137: 6. Type: *Aneuretus* Emery; monobasic.

Aneuretini, Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, 55: 71. (Description and inclusion of the Baltic amber genera *Protaneuretus* and *Paraneuretus*).

Aneuretini, Carpenter, 1930, Bull. Mus. Comp. Zool. Harv., 70: 39. (Description and inclusion of the genus *Mianeuretus* from the Florissant shales).

Aneuretinae (subfamily), Clark,[1] 1951, Formicidae of Australia, Genus *Myrmecia* (Commonwealth Sci. Indust. Res. Org., Australia), p. 16.

Diagnosis. (1) Clypeus broad, flat, and anteriorly emarginate, as in the Dolichoderinae.

(2) Petiole with an anterior peduncle at least as long as the basal portion of the node.

(3) Gaster completely lacking constrictions behind the first postpetiolar segment.

(4) Sting well-developed, sclerotized, and exsertile.

(5) Larva primitive in form, with well developed neck, large, sclerotized mandibles, and paxilliform maxillary palps and galeae.

(6) Pupae enclosed in cocoons; larvae with large, salient seriety-openings.

(7) Adult integument relatively thin and collapsible.

(8) Proventriculus generalized, with simple, mobile portal. Proventricular musele group *l. m.* 2 seemingly lacking.

(9) Fore-wing venation relatively generalized, but with the following specializations: first radial cross-vein lacking, Mf2 and Rs4 completely contracted.

Note on internal classification. The known genera of the subfamily include the nominate genus, with the single species described herein, and the extinct *Protaneuretus*, *Paraneuretus*, and *Mianeuretus*. Together, these four appear to constitute a single tribal entity, to be known as Aneuretini.

[1] While we are in agreement with Clark's elevation of the Aneuretini from tribal to subfamilial rank within the Formicidae, we consider most of his other subfamilial creations unwarranted, e.g., Nothomyrmeciinae, Eusphinctinae, Discothyrinae, and Odontomachinae.

DISTRIBUTION AND ECOLOGY

The present known distribution of *Aneuretus simoni* is shown in Figure 4. At present this species is known only from Ceylon. Here it is apparently more abundant in the southern part of the range, where it is associated with the rather limited rainforest area. Around Kandy and Peradeniya, the two localities from which the species had previously been recorded by other authors, Wilson searched in vain for it during a period of five days (July 10-14), before moving on into the more fruitful Ratnapura area.

The least disturbed forest within the Kandy-Peradeniya area is that of the Udawaddatekele Sanctuary, located just north of Kandy and representing the remains of the old royal gardens of the Kandy kings. This forest is relatively lush, with many large evergreen trees, but it is noticeably drier than the forests of the Ratnapura area and does not have a rainforest aspect. The impression that an insect collector gets here is that the ant fauna is diverse, but that the total population (of individuals) is rather sparse. Scarcity of individuals seems to be due in part to the scarcity of rotting wood on the ground, brought about in turn by the incessant activity of Singhalese wood-gatherers from Kandy. The few nesting sites left for wood-dwelling ants are further diminished by the dense population of termites, which on Ceylon are extremely abundant and more than able to hold their own in competition with the ants.

The following general observations were made with respect to the ant fauna of the Udawaddatekele Sanctuary. A great many, perhaps most, of the myrmicines, dolichoderines, and formicines nest on the ground in pieces of rotting wood, and forage both on the ground and up onto low vegetation. Ponerines nest primarily in pieces of rotting wood on the ground also, and confine their foraging to the ground. A high-arboreal fauna is not well developed, either in species or individuals. Judging from the number of individuals seen both in and away from nests, the dominant genera on the ground appear to be *Ponera* and *Pheidole,* followed by *Myrmicaria, Solenopsis* (*Diplorhoptrum*), and *Euponera* (*Mesoponera*), in that order. Also abundant, but considerably less so than the above genera, are *Leptogenys* (*s.*

lat.), *Paratrechina* (*Nylanderia*), and *Pseudolasius*. Among the low vegetation foragers, *Technomyrmex* leads, followed by *Tetramorium* (with *Xiphomyrmex*), and then *Polyrhachis* and *Camponotus* in that order. *Crematogaster* forages on the ground and up into the trees, but is rather scarce in this locality.

While not a single specimen of *Aneuretus simoni* was taken

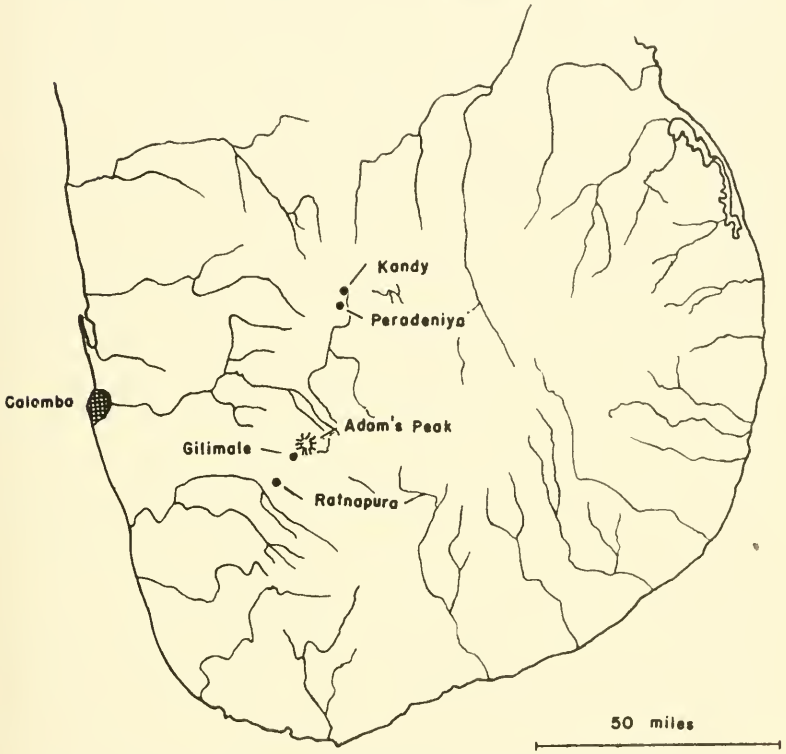


Fig. 4. Map of the southern half of Ceylon, showing the localities where *Aneuretus simoni* has been collected. The port of Colombo is included only for reference.

from the Kandy-Peradeniya forests, where it was most expected, it proved to be one of the dominant ants not far to the south, in the area between Ratnapura and Adam's Peak. At Ratnapura it was found to be extremely abundant in second-growth forest

around the city reservoir, and in similar "scrub" forest just two miles east of the city. It was also discovered in the extensive tract of rainforest that lies northeast of the village of Gilimale and near the foot of Adam's Peak.

The Gilimale forest was made the site of further intensive collecting in order to gain a picture of the natural environment of *Aneuretus*. Although far from being primary over most of its range, this forest is one of the least disturbed in Ceylon, and is probably not greatly different in elementary composition from the virgin rainforest of the nearby Sinharaja district.[1] In at least one spot remote from the main trails, the forest was found to approach what appeared to be a primary condition and exhibited several aspects of the "normal" tropical rainforest: trees forming several stories and a closed canopy, undergrowth sparse, and leaf litter and mold thin. Rotting wood is generally more abundant on the ground than at Kandy, but the total ant population is only slightly denser. The order of genus-dominance in the ant fauna is quite similar to that at Kandy, with the striking introduction of *Aneuretus* among the most prevalent components. On the ground, *Ponera* and *Pheidole* appeared to be the most abundant, as at Kandy. These are followed by *Myrmicaria*, *Aneuretus*, *Paratrechina* (*Nylanderia*), *Euponera* (*Mesoponera*), and *Euponera* (*Brachyponera*), in that order. Among the genera foraging on low vegetation, *Technomyrmex* is by far the most abundant, followed by *Polyrhachis* and *Camponotus*. *Tetramorium* occurs, but is far less common than at Kandy. *Crematogaster* is also present but relatively scarce.

In the Gilimale forest, colonies of *Aneuretus simoni* were most abundant at the edge of clearings (see Plate 3). This, coupled with the fact that the species is also successful in the scrubby forests around Ratnapura, may suggest that it is not naturally a dweller of the deep rainforests, but is adapted to clearings and more open forest types.

Some consideration should be given as to why *Aneuretus simoni* has been able to survive, and indeed flourish locally, in Ceylon, while in other parts of the world the aneuretines have faded to extinction. The general problems of extinction and range delimitation are certainly among the most complicated and least understood in biology, and to attempt to supply an

[1] For a description of the Sinharaja forest, see Baker (1938).

answer in this particular case with any tone of resoluteness would be unwarranted. Nevertheless, it may be of help to future students to mention a special condition of the Ceylon environment which appears to favor the survival of *Aneuretus*. This is the relatively weak development of the two ant genera *Pheidole* and *Crematogaster*. These two groups between them tend to occupy both the preferred nest site and food niche of *Aneuretus* (so far as these are known), and in many other tropical areas of the world they are overwhelming dominants of the ant fauna. On Ceylon, *Pheidole* is, to be sure, quite abundant, but relatively much less so than in comparable forests studied (by Wilson) in tropical Mexico and Melanesia, and it is represented by a smaller number of species. *Crematogaster* is very sparsely represented in both species and individuals.

It is also important to emphasize in this connection that since *Aneuretus simoni* is both ground-dwelling and primarily ground-foraging, its principal competition probably comes not from the dolichoderines, which are the phylogenetic successors of the aneuretines, but rather from the ponerines and myrmicines.

During the course of the field work in 1955 a total of 20 nests of *Aneuretus simoni* were collected. The number of individuals in each ranged from only two to over one hundred. Only two of the nests yielded dealate queens. One of these had, in addition to the queen, 94 minor workers, one major worker, and a quantity of eggs and small-to-medium larvae. The other contained what appeared to be an incipient colony, with eight relatively small minor workers and a quantity of all stages of brood in addition to the queen. Two other nests contained alate queens, and two contained males. Eight contained major workers, but there were never more than two of these to a nest. Nearly all of the twenty nests contained brood of various stages.

Eighteen of the 20 nests were in pieces of rotting wood on the ground. The pieces ranged in size from small twigs up to fallen tree-limbs three inches in diameter. In most cases the wood had decomposed to the extent that it could be easily crumbled in the hands. In two instances the *Aneuretus* were found beneath rather large rotting logs on the ground. No nests at all were found under rocks or in the open soil away from wood.

Numerous workers were found foraging during the daytime, during both overcast and sunny weather. They seemed to prefer shady places, and very likely were nocturnal also, although no field observations could be made during the night to check this supposition.[1] The great majority of workers encountered away from the nest were running over the surface of the ground; a few were taken on herbaceous plants and shrubs at heights of up to four feet.

Only a few observations were made on food habits. As might be expected of a primitive ant, *Aneuretus* is predaceous. On two occasions in the field, workers were found carrying entomobryid collembolans. In an artificial nest, workers of a colony accepted entomobryids readily and on one occasion captured about twenty of these insects in the course of one morning. Most significantly, the larvae were given the entomobryids directly, in the primitive ponerine fashion, and they fed on them separately from the workers. Workers in the artificial nest also accepted sugar water readily, and at each feeding this substance was distributed rapidly around the colony until all the adult individuals had full, distended gasters.

Adult trophallaxis was observed on several occasions. The donor opened its mandibles wide while the acceptor fed with closed mandibles from the donor's lower mouthparts. On one occasion a worker was seen donating to two of its sisters simultaneously. The occurrence of adult-larval trophallaxis was not investigated, although it is perhaps significant in this respect that callow workers in the artificial nest seemed extremely attentive of the brood, remaining close to it at all times.

In life the *Aneuretus* workers have the deceptive appearance of small yellow *Pheidole* minor workers, although to the experienced observer their general behavior is very un-myrmicine. They almost always keep their long petiole folded up against the posterior face of the propodeum, with the gaster correspondingly partly elevated. In foraging, they move at about an average gait for ants of comparable size; very roughly speaking, they are slower than most dolichoderines, such as *Technomyrmex albipes*, but faster than most ponerines, such as *Ponera coarctata*. Like many of the higher dolichoderines, they are much given to

[1] The workers of a colony maintained for a short time in an artificial nest foraged from the brood chamber into the uncovered food chamber during both the day and night.

halting abruptly at intervals, standing motionless for a moment, and then abruptly starting off again, often in another direction. When they are disturbed away from the nest, this behavior is intensified, with the workers dashing for a short distance, then halting and remaining perfectly still for a while, then dashing off again; under these conditions they show themselves capable of considerable speed and agility. When a nest is first broken open, the minor workers swarm out aggressively and run over any alien object offered them, but they do not attempt to bite or sting. Major workers seem to be more timid, and do not venture out in this fashion. The aggressiveness of the minor workers is usually short-lived, and they soon retreat back into the undisturbed part of the nest, leaving unprotected any brood which may happen to be in the exposed chambers. Later, they venture out singly to retrieve the brood.

LITERATURE CITED

BAKER, J. R.
1938. Rain-forest in Ceylon. Kew Bull., (1938): 9-16.

BROWN, W. L. and W. L. NUTTING
1950. Wing venation and phylogeny of the Formicidae (Hymenoptera). Trans. Amer. Ent. Soc., **75:** 113-132, 2 pls.

WHEELER, G. C. and J. WHEELER
1951. The ant larvae of the subfamily Dolichoderinae. Proc. Ent. Soc. Wash., **53:** 169-210, 4 pls., 1 text-fig.
1953. The ant larvae of the subfamily Formicinae. Ann. Ent. Soc. Amer., **46:** 126-171, 175-217, 6 pls., 2 text-figs.

PLATES

PLATE 1

A, Wings of queen. *B*, Wings of male. *C*, *G*, Queen. *D*, Male. *E*, *H*, Worker major. *F*, *I*, Worker minor.

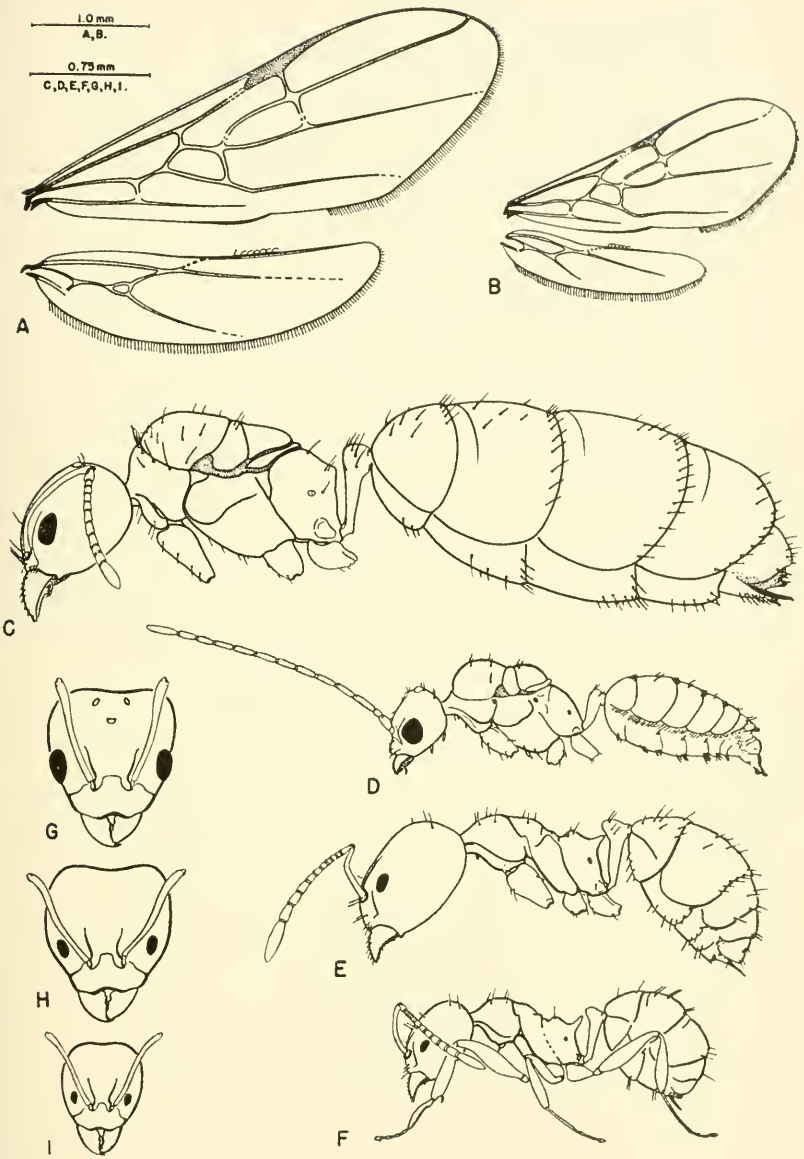


PLATE 1

PLATE 2

A, Male mandible. *B*, Worker mandible. *C*, Terminus of male abdomen, showing intact genitalia. *D-H*, Components of male genitalia isolated: *D*, subgenital plate (sternite IX); *E*, paramere; *F*, volsella; *G*, penis valve; *H*, tergites IX and X with pygostyles.

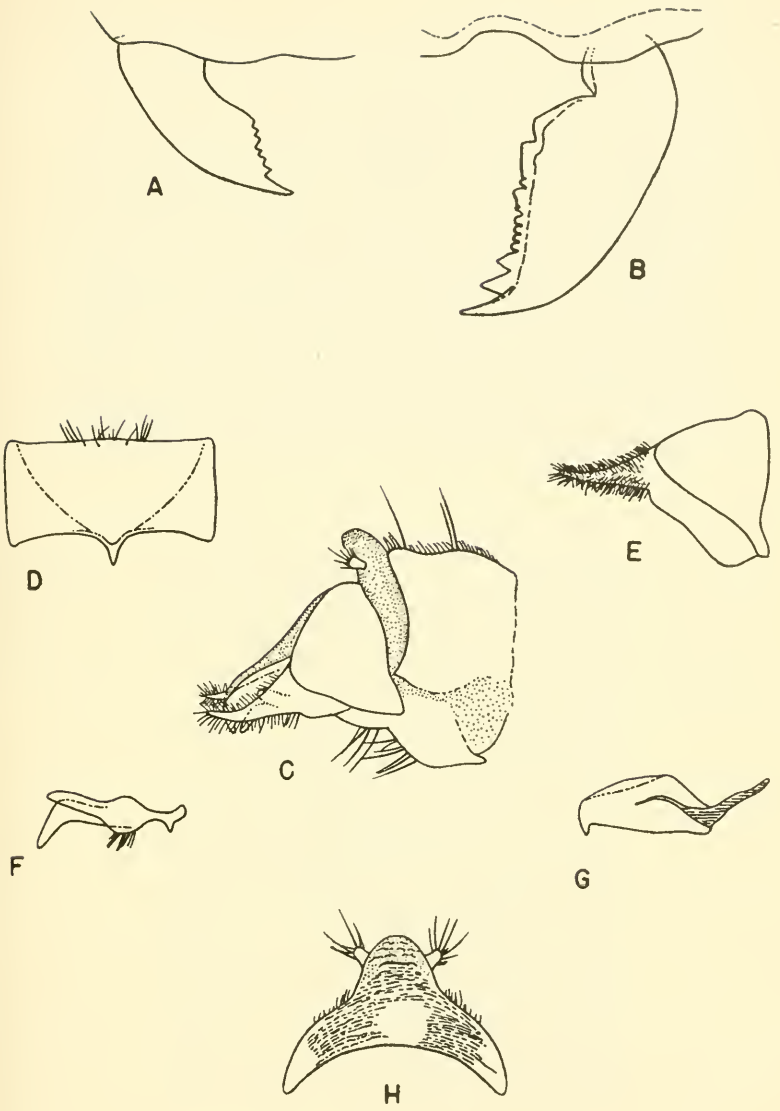


PLATE 2

PLATE 3

1. Rainforest near Gilimale, Ceylon; looking from a hill at the outskirts of Gilimale over the forest canopy toward the cloud — enveloped base of Adam's Peak in the distance.

2. Trail in the interior of the Gilimale forest, at a spot where *Aneuretus simoni* was one of the dominant ants.

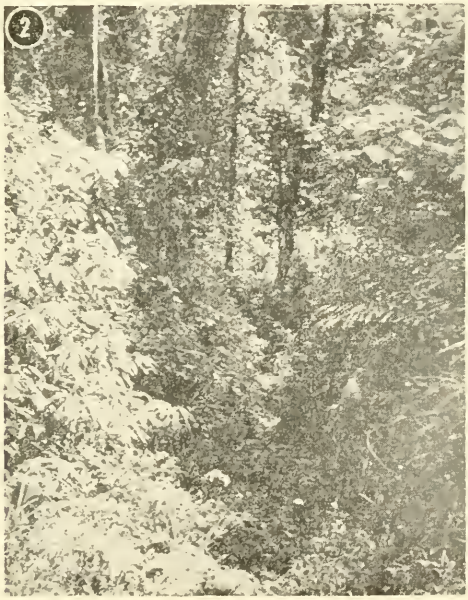


PLATE 3

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 4

THE TYPES OF NAIADES (MOLLUSCA: UNIONIDAE) IN THE MUSEUM OF COMPARATIVE ZOOLOGY

By Richard I. Johnson

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September, 1956

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 115.

Breviora (octavo) 1952 — No. 61 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899-1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 4

THE TYPES OF NAIADES (MOLLUSCA: UNIONIDAE) IN THE MUSEUM OF COMPARATIVE ZOOLOGY

By Richard I. Johnson

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September, 1956

No. 4 — *The Types of Naiades (Mollusca: Unionidae) in the Museum of Comparative Zoology*

By Richard I. Johnson

INTRODUCTION

The collection of Naiades of the Museum of Comparative Zoology had its beginning in 1863 when Louis Agassiz purchased the collection of J. G. Anthony of Cincinnati, Ohio. Anthony was primarily interested in North American fresh-water shells and, through voluminous correspondence and patience, he gathered together a very extensive number of authentic contemporary specimens. Like many pre-Darwinian naturalists, Anthony was akin to a stamp collector in his eagerness to possess accurate examples of each described species. Through his zeal, he laid the foundation, as the following list will illustrate, of a large and accurately labeled collection of type material. In his search for authentic specimens, Anthony anticipated the present day emphasis on the importance of types.

Agassiz not only purchased Anthony's shells, but induced him to become the museum's first Curator of Mollusks. As curator, Anthony continued to expand the collection. Anthony's chief rival as a collector of fresh-water shells was the rich and socially prominent Philadelphian, Isaac Lea, who devoted his very long life to the study of the Unionidae. While many of Anthony's own species have fallen into synonymy, he seemingly correctly recognized Lea as an inveterate splitter who described the slightest variation as a new species, and as an egotist who attempted to attach his name to every species that he shifted from the genus under which it was first assigned to a genus of his own making. It appears that the two rivals began cordially to dislike one another early in their careers, though there was a certain cold coöperation between them throughout their lives. The only primary types of Isaac Lea in the Museum of Comparative Zoology are those of species which Anthony sent to Lea, which proved to be new. Though Lea did not send Anthony any of his types, he did identify much of Anthony's material. These idiotypes and metatypes are included in this list because Lea was prone to base a species on a single example, and it was

thought that these subsequent identifications might be of interest, since they are what Lea *thought* he had described.

Lea described many species sent to him by C. M. Wheatley, and these shells are now in Union College, Schenectady, New York. Wheatley sent Anthony paratypes of many of these species. Among other people who sent Anthony types of Unionidae were: W. H. Benson, W. Theobold, W. B. R. H. Dunker, G. Von Dem Busch, Largilliert, and T. A. Conrad.

The next important acquisition was purchased in 1898 by Alexander Agassiz from R. E. Call. It consisted of land and fresh-water mollusks of the United States, and had formed the basis for Call's monographs of the Unionidae of Indiana and Arkansas and was rich in geographic series. In this series of several thousand lots are some types from Gerard Troost, though the main portion of Troost's collection went to the Rijksmuseum in Leiden, Holland.

It was a quarter of a century later before another large series of Unionidae was obtained. In 1926, W. J. Clench became Curator of Mollusks and he donated his collection to the museum. It contained the results of his own field efforts and duplicates from Bryant Walker of Detroit, Michigan. In 1928 and 1929, W. J. Clench and P. Okkelberg made collecting trips to Kentucky, Tennessee, Alabama, Georgia, and Florida. In 1933 W. J. Clench and H. Vander Schalie collected in Virginia, Tennessee, Alabama, and Georgia. The shells that were gathered on these trips were divided between the University of Michigan and the Museum of Comparative Zoology.

From 1914-1930 the Boston Society of Natural History parted with all of its Unionidae that were not from New England, and recently even the New England material has come to the Museum of Comparative Zoology. A number of lots from this collection, founded in 1830, have proved to be type material.

In 1930 Joseph Bequaert presented to the museum a series of African Unionidae and Mutelidae which contained types of most of the species he and H. A. Pilsbry described in 1927.

In 1946 while in China with the United States Navy, R. T. Abbott was able to purchase for the museum a remarkable set of types from the Musée Heude in Shanghai. These specimens formed the basis of R. P. Heude's work on the mollusks of the Province of Nanking.

In 1953-54 W. J. Clench and R. D. Turner in collaboration with the University of Florida extensively surveyed northern Florida and the adjacent areas of Georgia and Alabama, covering the rivers from the Escambia to the Suwannee. As a result of this work the Museum now has the largest collection of Unionidae from this area extant.

Probably the largest and finest assemblage of Unionidae in the world is that of the Museum of Zoology of the University of Michigan at Ann Arbor, Michigan. Certainly its series of North American forms is unrivaled. Its basis is the great collection of Bryant Walker which itself consisted of many other famous aggregations including those of J. Lewis, E. R. Showalter, and L. S. Frierson. The latter collection (see Frierson, L. S., 1927, p. 5) was made up from the labors of other well known malacologists.

Probably ranking next in size is the collection in the Museum of Comparative Zoology, which in addition to containing the Unionidae described herein, has been painstakingly added to by W. J. Clench through his efforts in the field and by world-wide exchange. The geographic series is being constantly increased through the devoted interest of H. D. Athearn and many others.

The United States National Museum at Washington, District of Columbia, while lacking the extensive geographic series of the above-mentioned institutions, doubtless has the largest number of types of Naiades in the world, containing as it does the life work of Isaac Lea and numerous lesser collections such as that of B. H. Wright.

The Academy of Natural Sciences of Philadelphia has a relatively small series, but contains many of the types of T. Say, T. A. Conrad and the so-called Pulson-Rafinesque types.

These are the most important collections in the United States, but there are also valuable ones in the Chicago Natural History Museum, Chicago Academy of Sciences, and American Museum of Natural History in New York City.

The Senckenberg Museum in Frankfurt am Main, Germany, has a large and important collection of Naiades, especially from the Far East, which was greatly enhanced in value through years of labor by Fritz Haas. The Berlin, Brussels, Paris, and British museums all contain important types, as do many of the smaller continental museums at Rouen, France, and Geneva,

Switzerland. In general, the European collections have smaller series and fewer records. This observation is based on the author's rather hasty visits to most of the above-mentioned museums.

As few of the earlier authors designated holotypes, we have been content to call the types syntypes or cotypes. In cases where one specimen has been well figured or we have been able to locate the measured specimen, we have regarded these as either holotypes or lectotypes, and considered any other specimens in the type lot as paratypes. An allotype is a paratype of the opposite sex to the holotype. Idiotypes are merely specimens identified by the author of a species, and metatypes are topotypes (from the original locality) identified by the author. The importance of these last two categories can be questioned, but in the absence of primary types, which can not be located or have been destroyed, or in cases where the species was based on a unique specimen, they have some value.

BIBLIOGRAPHY

Clench, W. J., 1936. The collection of mollusks. [*in*] Notes concerning the history and contents of the Museum of Comparative Zoology. Harvard College, Cambridge, Massachusetts: 69-72.

Frierson, L. S., 1927. A classified and annotated check list of the North American Naiades. Waco, Texas: 5-8.

Lea, Isaac, 1834-1874. Observations on the Genus Unio. Philadelphia, **1-13.**

Simpson, C. T., 1900. Synopsis of the Naiades, or pearly freshwater mussels. Proc. United States Nat. Mus., **22:** 504-515.

Turner, R. D., 1946. John Gould Anthony, with a bibliography and catalogue of his species. Occasional Papers on Mollusks, Cambridge, Massachusetts, **1** (8): 81-94.

ACKNOWLEDGMENTS

The author is especially indebted to Drs. W. J. Clench and R. D. Turner for their ever willing help and encouragement, which has meant time out from their own busy schedules of research. Thanks are also extended to Mr. H. D. Athearn for his willing aid in certain curatorial tasks connected with this work.

A List of the Types of Recent Naiades in the Museum of Comparative Zoology in 1956, with their Original References and Type Localities

The following list is arranged alphabetically by species, giving the original author, the year and place of publication of its original description, the type locality and collector (in parenthesis), the kind of type material — paratype or idiotype, etc. — and finally the MCZ number and the source from which it came to this museum. In the case of the species described by Isaac Lea, we have only given the original reference whereby he fixed the date of publication, and the later reference to the particular volume of the "Observations on the Genus Unio" in which Lea reprinted all of his descriptions and plates which originally appeared in other journals. All locality data, in brackets, contained in this report are additions to already published records and have been obtained from original labels or other sources.

Dr. J. Bequaert has kindly afforded notes on the present status of certain species which he described with Dr. H. A. Pilsbry in 1927.

The initials PANSP refer to the Proceedings of the Academy of Natural Sciences of Philadelphia, JANSP to the Journal of the same society, Tr. APS to the Transactions of the American Philosophical Society, Pr. APS to the Proceedings of the same society, Obs. to Observations on the Genus Unio, and MCZ to Museum of Comparative Zoology.

ablatus [*sic*] Lea, *Unio:* 1863, PANSP, p. 193; 1867, Obs. 11, p. 17, pl. 4, fig. 10 [name changed to *oblatus*] (Long Creek, Gaston County, North Carolina, C. M. Wheatley; North Carolina, J. G. Anthony) 2 Paratypes MCZ 150806 ex J. G. Anthony.

abortivus Heude, *Unio:* 1883, Conch, Fleuv. Nanking, Part 8, pl. 63, fig. 124 (certains torrents ou ruisseaux du Ts' ing-yang hieu, province du Ngan-houé [China]) 4½ Paratypes MCZ 167255 ex Musée Heude.

acutissimus Lea, *Unio:* 1831, Tr. APS, **6**, p. 89, pl. 10, fig. 18; 1834, Obs. **1**, p. 99, pl. 10, fig. 18 (Alabama River, Judge Tait) 4 Idiotypes MCZ 178887.

aethiopiformis 'von Ihering' Simpson, *Unio:* 1914, Desc. Cat. Naiades, Detroit, Michigan, **3,** p. 1312 [*nomen nudum*] 2 Cotypes MCZ 19236, ex S. Putzeys coll'n.

affinis Lea, *Unio:* 1852, Pr. APS, **5,** p. 251; 1852, Obs., **5,** p. 27, pl. 19, fig. 26 (Alexandria, Louisiana, T. Hale) 1 Idiotype MCZ 178885.

aheneus Lea, *Unio:* 1843, Desc. 12 Uniones [no pagination]; 1848, Obs., **4,** p. 38, pl. 41, fig. 9 (Black Creek, Florida, S. B. Buckley), 1 Idiotype MCZ 178713.

anceps Deshayes, *Unio:* 1874, Nouvelles Archives du Museum, Paris, France, **10,** p. 127, pl. 6, figs. 9-12 (sur les rivages du Mekong, Cambodia dans le sable fin, Jullien) 1 Cotype MCZ 187536 ex G. P. Deshayes.

andrewsii Marsh, *Quadrula:* 1902, Nautilus, **15,** p. 115; 1902, Nautilus, **16,** p. 8, pl. 1, upper two figs. as *Q. andrewsae* (Holston River, Tennessee, Mrs. Geo. Andrews) 1 Paratype MCZ 134060 ex B. Walker coll'n.

appressus Lea, *Unio:* 1871, PANSP, p. 189; 1874, Obs., **13,** p. 16, pl. 3, fig. p. 8, pl. 1, upper two figs. as *Q. audrewsae* (Holston River, Tennessee. Holston River, Miss Law and C. M. Wheatley) 1 Paratype MCZ 37102 from Miss Law in the E. R. Mayo coll'n. ex Boston Soc. Nat. Hist.

approximus Lea, *Unio:* 1845, Pr. APS, **4,** p. 164; 1848, Obs., **4,** p. 48, pl. 5, fig. 13 (Red River at Alexandria, Louisiana, J. Hale) 2 Idiotypes MCZ 178900.

aquilus Lea, *Unio:* 1857, PANSP, p. 172; 1858, Obs., **6,** p. 92, pl. 20, fig. 72 (Flint River, near Macon, Georgia, J. C. Plant; Chattahoochee River at Roswell, Georgia, N. A. Pratt, Jr.) 3 Idiotypes MCZ 124884.

arcus Conrad, *Unio:* 1834, Amer. Jour. Sci., **25,** p. 340, pl. 1, fig. 8 (Alabama River) 1 Idiotype MCZ 178767.

argenteus Lea, *Unio:* 1841, Pr. APS, **2,** p. 82; 1842, Obs., **3,** p. 80, pl. 25, fig. 57 (Holston River, East Tennessee, Dr. Troost and Mr. S. M. Edgar) 4 Idiotypes MCZ 178813.

armathwaitensis B. H. Wright, *Unio gibbosus:* 1898, Nautilus, **11,** p. 123 (A branch of the South Fork of the Cumberland River at Armathwaite, Fentress County, Tennessee) 1 Paratype MCZ 20167 from B. H. Wright ex L. S. Frierson.

ascia 'Benson' Hanley, *Unio:* 1856, Cat. Recent Bivalve Shells, p. 385, pl. 23, fig. 20 (Penang [Straits Settlements]). Listed by Simpson, 1914, Desc. Cat. Naiades, Detroit, Michigan, **3,** p. 1192 as indeterminate. Lectotype, here selected, MCZ 17046, pl. 2, fig. 2, ex W. H. Benson.

askewi Marsh, *Unio:* 1896, Nautilus, **10,** p. 91; 1897, Nautilus, **10,** pl. 1, figs. 3, 4 (Village Creek, Hardin County, Texas, A. G. Wetherby; Sabine River, Texas, H. G. Askew) 2 Paratypes MCZ 30555 from the latter locality from W. A. Marsh, ex B. Walker coll'n.

asperatus Lea, *Unio:* 1861, PANSP, p. 61; 1862, Obs., **8,** p. 72, pl. 7, fig. 218 (Alabama River, Claiborne, Alabama, Judge Tait; Coosa River, Alabama, E. R. Showalter) 1 Idiotype MCZ 178830.

auroreus Heude, *Unio:* 1883, Conch. Fleuv. Nanking, Part 8 ,pl. 57, fig. 106 (A l'origine des torrents Ning-Kouo hien, Kien-té hien [China]) 4 Paratypes MCZ 167254 ex Musée Heude.

australis Simpson, *Lampsilis:* 1900, PANSP, p. 75, pl. 2, fig. 2, (Little Patsaliga Creek, Southeastern Alabama) 1 Paratype MCZ 20154 ex L. S. Frierson.

averillii B. H. Wright, *Unio:* 1888, PANSP, p. 115, pl. 3, fig. 3 (Lake Ashby, Volusia County, Florida) 16 Paratypes MCZ 134058 and 190123 from B. H. Wright ex B. Walker coll'n.

balonnensis Conrad, *Unio:* 1850, PANSP, p. 10; 1854, JANSP, **2,** p. 295, pl. 26, fig. 3 ([Balonne River, Queensland, Australia]) 1 Paratype MCZ 72078 ex Acad. Nat. Sci. Philadelphia.

bardwelli Clench, *Hyridella* (*Hyridella*): 1934, Jour. of Conch., **20,** p. 89, pl. 2, figs. 1-5 (Lower Reaches of the Glenelg River, Kimberly Division, Western Australia, Beresford Bardwell) Holotype MCZ 41999; 12 Paratypes MCZ 42000.

barnesianus Lea, *Unio:* 1838, Tr. APS, **6,** p. 31, pl. 10, fig. 26; 1838, Obs., **2,** p. 31, pl. 10, fig. 26 (Cumberland River, Tennessee, Prof. Troost) Holotype MCZ 5001 from Troost, ex R. E. Call coll'n. Lea based this species on one specimen in the Troost collection. This is presumably that specimen, though it is slightly smaller than the measurements given by Lea. 3 Idiotypes MCZ 178819.

beaverensis Lea, *Unio:* 1868, PANSP, p. 161; 1869, Obs., **12,** p. 57, pl. 44, fig. 109 (Beaver Creek and Long Creek, North Carolina, C. M. Wheatley; and Carter's Creek, Geo. J. Postell) 2 Paratypes MCZ 178769 ex C. M. Wheatley. Localities not separated.

bellua Morelet, *Anodonta:* 1866, Rev. et Mag. Zool., (2) **18,** p. 167 (Lacu Toui-Sap, Cambodia) Lectotype, here selected, MCZ 175610, Pl. 1, fig. 1, ex A. Morelet. This is the first time that this species has been figured.

berthae Ortmann, *Diplodon:* 1921, Mem. Carnegie Mus. Pittsburgh, Pa., **8,** p. 528, pl. 38, figs. 1-4, [gills], pl. 46, fig. 6 (Rio Jacuhy, Cachoeira, Rio Grande do Sul, Brazil, J. D. Haseman) 1 Cotype MCZ 100974 ex Carnegie Museum.

bigbyensis Lea, *Unio:* 1841, Pr. APS **2,** p. 30; 1842, Obs., **3,** p. 75, pl. 22, fig. 51 (Big Bigby Creek, Maury County, Tennessee, T. R. Dutton) 3 Idiotypes MCZ 178816.

birgei Baker, *Anodontoides:* 1923, Nautilus, **36,** p. 123; 1928, Bull. Univ. Wisconsin, serial 1527, p. 180, pl. 68, figs. 1-4 (Sturgeon Bay, Door County, below railroad bridge, Wisconsin) 4 Paratypes MCZ 89212.

bisselianus Lea, *Unio:* 1867, PANSP, p. 81; 1869, Obs., **12,** p. 37, pl. 37, fig. 90, (Bissel's Pond, Charlotte, North Carolina, C. M. Wheatley) 4 Paratypes MCZ 178690 and 202939 ex C. M. Wheatley.

blandianus Lea, *Unio:* 1856, PANSP, p. 263; 1858, Obs., **6,** p. 65, pl. 11, fig. 47 (Othcalooga Creek, Gordon County, Georgia, Bishop Elliott) 2 Idiotypes MCZ 178786.

blandingianus Lea, *Unio:* 1934, Tr. APS, **5,** p. 101, pl. 15, fig. 44; 1834, Obs., **1,** p. 213, pl. 15, fig. 44 (St. John's River, ? [*sic*] Florida, Dr. Blanding) 2 Paratypes MCZ 178689, ex Dr. Blanding.

bolli Call, *Unio:* 1881, Amer. Natur., **15,** p. 390 (Colorado River [Austin] Texas) Lectotype, here selected, MCZ 5017, Pl. 1, fig. 2. 15 Paratypes MCZ 5016.

borealis A. F. Gray, *Unio:* 1882, Tr. Ottawa Field Nat. Club, No. 3, p. 53, 3 figs. (Ottawa River at Duck Island; Leamy's Lake, near Hull, Quebec, Canada) Lectotype, here selected, MCZ 51470 from the former locality ex A. F. Gray coll'n.

bournianus Lea, *Unio:* 1840, Pr. APS, **1,** p. 288; 1842, Obs., **3,** p. 51, pl. 15, fig. 28 (Scioto River near Chillicothe, Ohio, A. Bourne) 1 probable Paratype MCZ 178833. The original label reads, "(unique) Genuine rec. from the original finder Henry Moores [*sic*] who sent it to Lea for description."

boykinianus Lea, *Unio:* 1840, Pr. APS, **1,** p. 288; 1842, Obs., **3,** p. 46, pl. 13, fig. 22 (Chattahoochee River, Columbus, Georgia, Dr. Boykin) 3 Idiotypes MCZ 141087.

breviculus Call, *Unio:* 1887, Pr. U. S. Nat. Mus., **10,** p. 499, pl. 28 (Currant River, Shannon County, Missouri, and in Jack's Fork and Big Creek, tributaries to it.) Figured Holotype MCZ 5020, from Jack's Fork; figured Allotype MCZ 5023. In addition there are extensive lots of paratypes from each locality. Ex R. E. Call coll'n.

buckleyi Lea, *Unio:* 1843, Desc. 12 Uniones [no pagination]; 1848, Obs., **4,** p. 34, pl. 39, fig. 2 (Lake George and Lake Monroe, Florida, S. B. Buckley) 3 Idiotypes MCZ 178723.

buddianus Lea, *Unio:* 1843, Desc. 12 Uniones [no pagination]; 1848, Obs., **4**, p. 35, pl. 40, fig. 5 (Lake George and Lake Monroe, Florida, S. B. Buckley) 1 Idiotype MCZ 178726.

burkensis Lea, *Unio:* 1859, PANSP, p. 112; 1859, Obs., **7**, p. 33, pl. 27, fig. 95 (Buckhead Creek, Burke County, Georgia, Bishop Elliot) 5 Idiotypes MCZ 150810.

bursa-pastoris B. H. Wright, *Unio:* 1896, Nautilus, **9**, p. 133, pl. 3 (Powell River, Virginia) 3 Idiotypes MCZ 30574 from the Clinch River, Tennessee.

buxtoni B. H. Wright, *Unio:* 1897, Nautilus, **11**, p. 55; figured by Simpson, 1900, PANSP, p. 80, pl. 1, fig. 6 (Lakelets of Monroe County, Florida) 2 Paratypes MCZ 20173 from B. H. Wright ex L. S. Frierson.

caeruleus Lea, *Unio:* 1831, Tr. APS, **4**, p. 95, pl. 13, fig. 25; 1834, Obs. **1**, p. 105, pl. 13, fig. 25 (River Hoogly, Hindostan [India], G. W. Blakie) 3 Idiotypes MCZ 175565.

californiensis Lea, *Anodonta:* 1852, Tr. APS, **10**, p. 286, pl. 25, fig. 47; 1852, Obs., **5**, p. 42, pl. 25, fig. 47 (Rio Colorado, California, J. L. Le Conte) 3 Paratypes MCZ 161905 ex I. Lea.

caliginosus Lea, *Unio:* 1845, Pr. APS, **4**, p. 165; 1848, Obs., **4**, p. 53, pl. 7, fig. 21 (Red River, at Alexandria, Louisiana, J. Hale) 2 Idiotypes MCZ 178894.

capsaeformis Lea, *Unio:* 1834, Tr. APS, **6**, p. 31, pl. 2, fig. 4; 1834, Obs., **1**, p. 143, pl. 2, fig. 4 (Cumberland River [Tennessee], W. Cooper) Holotype MCZ 178570 ex W. Cooper; 3 Idiotypes MCZ 178568.

cariosus Say, *Unio:* 1817, Nicholson's Encyclopedia, **2** [no pagination] pl. 3, fig. 2 (Delaware and Schuylkill rivers; [Susquehanna River] Wilkesbarre [Pa.]) Neoholotype MCZ 178839, Neoallotype MCZ 151644, selected by Johnson 1947, Occ. Papers on Mollusks, **1**, p. 148, pl. 19, figs. 1, 2. The type locality was limited to the Schuylkill River, near Philadelphia, Pa.

castaneus Lea, *Unio:* 1831, Tr. APS, **4**, p. 91, pl. 11, fig. 27; 1834, Obs., **1**, p. 91, pl. 11, fig. 27 (Alabama River [Alabama], Judge Tait) 3 Idiotypes MCZ 178925.

catawbensis Lea, *Unio:* See under *wheatleyi* Lea, *Unio.*

celtiformis Heude, *Unio:* 1874, Jour. de Conch., **22**, p. 113; 1875, Conch. Fleuv. Nanking, Part 1, pl. 1, fig. 4 (Kiang-Si, dans la rivière de Fou-tcheou [China]) 1 Paratype MCZ 167253 ex Musée Heude.

cerinus Conrad, *Unio:* 1838, Monography Family Unionidae, Part 11, p. 95, pl. 52 (Probably inhabits the waters of Louisiana not far from New Orleans) 1 Idiotype MCZ 178781.

chattanoogaensis Lea, *Unio:* 1858, PANSP, p. 166; 1859, Obs., **7.** p. 27, pl. 25, fig. 90 (Chattanooga, Tennessee, T. Stewardson; Etowah River, G. White; Coosawattee and Oostenaula Rivers, Bishop Elliott) 6 Idiotypes MCZ 178791.

chinensis Lea, *Unio:* 1868, PANSP, p. 150; 1869, Obs., **12.** p. 85, pl. 53, fig. 138 (Hong Kong, China) Holotype MCZ 175567 from Yale College, New Haven, Conn. ex J. G. Anthony.

cincinnatiensis Lea, *Unio:* 1840, PANSP, p. 285; 1842, Obs., **3.** p. 32, pl. 8, fig. 4 (Ohio River at Cincinnati [Ohio], T. G. Lea) 3 Idiotypes MCZ 23604.

claibornesis Lea, *Unio:* 1838, Tr. APS, **6.** p. 105, pl. 24, fig. 115; 1838, Obs., **2.** p. 105, pl. 24, fig. 115 (Alabama River, near Claiborne [Alabama], Judge Tait) 1 Idiotype MCZ 146969.

clintonensis Simpson, *Ptychobranchus:* 1900, PANSP, p. 79, pl. 5, fig. 3 (Archie's Fork of Little Red River, near Clinton, Arkansas) 11 Paratypes MCZ 192371 from C. T. Simpson ex B. Walker coll'n.

compactus Lea, *Unio:* 1859, PANSP, p. 154; 1859, Obs., **7.** p. 36, pl. 28, fig. 98 (Etawah River, Georgia, Bishop Elliott and Rev. G. White; and Connasauga River, Bishop Elliot) 2 Idiotypes MCZ 178905.

concestator Lea, *Unio:* 1857, PANSP, p. 31; 1858, Obs., **6.** p. 66, pl. 12, fig. 48 (Creeks, near Columbus, Georgia, Bishop Elliott and Dr. Lewis) 5 Idiotypes MCZ 178926.

confertus Lea, *Unio:* 1834, Tr. APS, **5.** p. 103, pl. 16, fig. 47; 1834, Obs., **1.** p. 215, pl. 16, fig. 47 (Santee Canal, South Carolina, Prof. Ravenel) 2 Idiotypes MCZ 178875.

connasaugaensis Lea, *Margaritana:* 1857, PANSP, p. 135; 1859, Obs., **7.** p. 47, pl. 32, fig. 113 (Connasauga River, one of the head waters of the Alabama River, in Gilmer County, Georgia, Bishop Elliott; Tennessee, J. G. Anthony) 2 Paratypes MCZ 146985 ex J. G. Anthony.

conradicus Lea, *Unio:* 1834, Tr. APS, **5.** p. 63, pl. 9 fig. 23; 1834, Obs., **1.** p. 175, pl. 9, fig. 23 (Hab . . ., Prof. Troost) 3 Idiotypes MCZ 178931 from Virginia.

conspicuus Lea, *Unio:* 1872, PANSP, p. 156; 1874, Obs., **13.** p. 38, pl. 11, fig. 31 (Yadkin River, near Salisbury, North Carolina, C. M. Wheatley) 2 Paratypes MCZ 178878 ex C. M. Wheatley.

cor Conrad, *Unio:* 1834, New Fresh Water Shells of the United States, p. 28, pl. 3, fig. 3 (Inhabits Elk and Flint Rivers, Alabama) Holotype MCZ 178792 purchased by J. G. Anthony. Frierson figured the "type" of this species (1916, Nautilus, **29**, pl. 3) and claimed later (1927, Check list North American Naiades, Waco, Texas, p. 59) that the shell figured by Conrad was not the one described, whereupon he selected the "described" shell as the type. In his first article Frierson mentions that Dr. Pilsbry thought that Conrad's figure of the shell was a slightly older shell, but of the same species. In either case, the name must rest on the figured Holotype which is here reproduced, Pl. 2, fig. 3, as the original figure is poor.

crebristriata Anthony, *Monocondylaea:* 1865, Amer. Jour. Conch., **1**, p. 205, pl. 18, fig. 1 (Pegu, British Burma) Holotype MCZ 161872, 30 Paratypes MCZ 178935.

crispata Gould, *Unio:* 1843, Pr. Boston Soc. Nat. Hist., **1**, p. 141 (Tavoy, British Burma, Rev. F. Mason) 3 Idiotypes MCZ 175564.

crocatus Lea, *Unio:* 1841, Pr. APS, **2**, p. 31; 1842, Obs., **3**, p. 76, pl. 22, fig. 52, (Savannah River, Georgia, T. R. Dutton) 1 Idiotype MCZ 146988.

cumberlandicus Lea, *Unio:* 1838, Tr. APS, **6**, p. 25, pl. 7, fig. 19; 1838, Obs., **2**, p. 25, pl. 7, fig. 19 (Cumberland River, Tennessee. Prof. Troost) 1 Idiotype MCZ 178928; 3 Idiotypes MCZ 178899 from the Clinch River, Tennessee.

cumingii Lea, *Monocondylaea:* 1850 [1851] Pr. Zool. Soc. London, p. 199 [as *Anodonta cumingii*]; 1860, Obs., **7**, p. 53, pl. 33, fig. 114 (Malacca [Straits Settlements], H. Cuming) 2 Paratypes MCZ 175582 ex H. Cuming.

cuneolus Lea, *Unio:* 1840, Pr. APS, **1**, p. 286; 1842, Obs., **3**, p. 31, pl. 7, fig. 3 (Holston River, Tennessee, S. M. Edgar) 7 Idiotypes MCZ 178799.

cunninghami B. H. Wright, *Unio:* 1883, PANSP, p. 58, pl. 1, figs. 1-4 (Lakes of Sumter County, Florida) 3 Cotypes MCZ 178700 ex B. H. Wright.

curtus Lea, *Unio:* 1859, PANSP, p. 112; 1862, Obs., **8**, p. 107, pl. 18, fig. 253 (Tombigbee River, Columbus, Mississippi, Wm. Spillman) 1 Idiotype MCZ 178812 from Selma, Alabama.

dactylus Lea, *Unio:* 1840, Pr. APS, **1**, p. 287; 1842, Obs., **3**, p. 34, pl. 9, fig. 7 (Cany Fork River, Tennessee, S. M. Edgar) 1 Idiotype MCZ 178910.

dakota Frierson, *Anodonta:* 1910, Nautilus, **23**, p. 113, pl. 10 (Ulvers Point, Clear Lake, Deuel County, South Dakota, W. H. Over) 1 Paratype MCZ 134118 ex B. Walker coll'n.

dalli B. H. Wright, *Unio:* 1888 PANSP, p. 119, pl. 4, fig. 1 (Lake Beresford, Volusia County, Florida) 5 Idiotypes MCZ 178704.

dariensis Lea, *Unio:* 1842, Tr. APS, **8,** p. 246, pl. 26, fig. 61; 1842, Obs., **3,** p. 84, pl. 26, fig. 61 (Near Darien, Georgia, J. H. Couper) 2 Idiotypes MCZ 28330.

datus Lea, *Unio:* 1868, PANSP, p. 161; 1869, Obs., **12,** p. 59, pl. 44, fig. 3 (Paw Creek, Beaver County and Long Creek, North Carolina, C. M. Wheatley) 2 Paratypes MCZ 178710 ex C. M. Wheatley. Localities not separated.

decisa Lea, *Unio:* 1831, Tr. APS, **4,** p. 92, pl. 12, fig. 23; 1834, Obs., **1,** p. 102, pl. 12, fig. 23. (Alabama River, Judge Tait) 1 Idiotype MCZ 178797.

delphinus Gruner, *Unio:* 1841, Archiv für Natur., **1,** p. 276, pl. 11, figs. 1, 1a-c. (in songi flumine Malacca [Straits Settlements]) 2 Cotypes MCZ 186371 ex C. B. Adams coll'n. Apparently G. Von dem Busch of Bremen sent specimens of this species to C. B. Adams and Isaac Lee with the locality "New Holland?". It is with this locality and under Gruner's name that Lea described the shell the year following Gruner (1842, Tr. APS, **8,** p. 218, pl. 17, fig. 35), apparently unaware that Gruner had already published the name. After Lea's paper went to press, Von dem Busch sent Lea the correct locality. Thus, the Adams specimens of *delphinus* Gruner were those distributed by Gruner through Von dem Busch prior to publication.

depygis Conrad, *Unio:* 1866, Amer. Jour. Conch., **2,** p. 107, pl. 10, fig. 1 (Harpeth River, Tennessee W. H. DeCamp) Type lost, see Johnson, 1948, Nautilus, **62,** p. 102.

deviatus Anthony, *Unio:* 1865, Amer. Jour. Conch., **1,** p. 156, pl. 12, fig. 2 (Tennessee) Holotype MCZ 161859.

diazensis S. H. Wright, *Unio:* 1897, Nautilus, **11,** p. 5 (Lake Diaz, Volusia County, Florida) 2 Cotypes MCZ 37314 from B. H. Wright from the E. W. Roper coll'n., ex Boston Soc. Nat. Hist.

dignatus Lea, *Unio:* 1863, PANSP, p. 189; 1867, Obs., **11,** p. 55, pl. 17, fig. 48 (River Tigris at Bagdad [Iran], C. M. Wheatley) 2 Paratypes MCZ 161975 ex C. M. Wheatley.

dimotus Lea, *Unio:* see under *sumatrensis* Lea.

discoidea Lea, *Unio:* 1834, Tr. APS, **5,** p. 75, pl. 11, fig. 33; 1834, Obs., **1,** p. 187, pl. 11, fig. 33 (China) 1 Idiotype MCZ 175574.

discrepans Lea, *Unio:* 1860, PANSP, p. 92; 1860, Obs., **8**, p. 22, pl. 55, fig. 165 (North Alabama, Prof. Tuomey) 2 Idiotypes MCZ 178918.

dispar Lea, *Unio:* 1860, PANSP, p. 305; 1860, Obs., **8**, p. 9, pl. 51, fig. 153 (Columbus, Georgia, Bishop Elliott and G. Hallenbeck) 2 Idiotypes MCZ 178932.

distans Anthony, *Unio:* 1865, Amer. Jour. Conch., **1**, p. 156, pl. 13, fig. 2 (Ohio) Holotype MCZ 146978.

dolabelloides Lea, *Unio:* 1840 PANSP, p. 288; 1842, Obs., **3**, p. 53, pl. 15, fig. 31 (Holston River, Tennessee, Prof. Troost) 1 Paratype MCZ 25254 from G. Troost ex R. E. Call coll'n.

dolabraeformis Lea, *Unio:* 1838, Tr. APS, **6**, p. 103, pl. 24, fig. 113; 1838, Obs., **2**, p. 103, pl. 24, fig. 113 (Altamaha River, Liberty County, Georgia, Lewis Leconte; Altamaha River, near Darien, Georgia, Prof. Ravenel) 1 Idiotype MCZ 28283.

dorei B. H. Wright, *Unio:* 1888, PANSP, p. 115, pl. 3, fig. 1 (Lake Monroe, Florida) 4 Paratypes MCZ 178721 ex B. H. Wright.

downiei Lea, *Unio:* 1858, PANSP, p. 166; 1859, Obs., **7**, p. 28, pl. 25, fig. 91 (Buck Lake, a bayou of Satilla River, Wayne County, Georgia, T. C. Downie) 2 Paratypes MCZ 178716, received prior to publication.

edgarianus Lea, *Unio:* 1840, Pr. APS, **1**, p. 288; 1842, Obs., **3**, p. 52, pl. 15, fig. 30 (Holston River, Tennessee, Prof. Troost and Dr. Currey; Tennessee River, at Florence, Alabama, Mr. Dutton) 5 Idiotypes MCZ 178821 from the Sequatchee River, Tennessee.

elliottii Lea, *Margaritana:* 1858, PANSP, p. 138; 1859, Obs., **7**, p. 44, pl. 31, fig. 108 (Chattahoochee River near Columbus, Georgia) 1 Idiotype MCZ 146990.

ellipticum Conrad, *Pseudodon:* 1865, Amer. Jour. Conch., **1**, p. 352, pl. 25, fig. 1 (Cambodia, C. M. Wheatley) Holotype MCZ 175575 ex C. M. Wheatley.

excavatus Lea, *Unio:* 1857, PANSP, p. 32; 1858, Obs., **6**, p. 71, pl. 13, fig. 52 (Othcalooga Creek, Gordon County, Georgia, Bishop Elliott; Etowah, Georgia, Rev. G. White; Claiborne, Alabama, Judge Tait) 3 Idiotypes MCZ 23602.

exiguus Lea, *Unio:* 1840, Pr. APS, **1**, p. 287; 1842, Obs., **3**, p. 29, pl. 7, fig. 1 (Chattahoochee River, Columbus, Georgia, Dr. Boykin) 3 Idiotypes MCZ 178912.

fabula Lea, *Margaritana:* 1838, Tr. APS, **6**, p. 44, pl. 13, fig. 39; 1838, Obs., **2**, p. 44, pl. 13, fig. 39 (Cumberland River, Tennessee, Prof. Troost) 5 Idiotypes MCZ 146482.

falcata Gould, *Alasmidonta:* 1850, Pr. Boston Soc. Nat. Hist., **3**, p. 294; 1852, U. S. Expl. Exped., **12**, p. 433, figs. 545-545b (Wallawalla, Spokane, Wahlamet, etc., J. Drayton; Oregon and Upper Sacramento River, California, Dr. Pickering) ½ Cotype MCZ 155763, labeled "Oregon District" ex Smithsonian Institution; 3 Cotypes MCZ 28296 labeled "California" ex A. A. Gould.

falcatus Higgins, *Mycetopus:* 1868, Pr. Zool. Soc. London, p. 179, pl. 14, fig. 6 (Forest streams near Chyavetas, Upper Amazons [Brazil], E. Bartlett) 1 Cotype MCZ 74218 ex R. F. Geale. This specimen agrees with the plate and may well be the one figured.

fallax Lea, *Unio:* 1857, PANSP, p. 32; 1858, Obs., **6**, p. 79, pl. 15, fig. 59 (Streams near Columbus, Georgia, Bishop Elliott; and French Broad River, Tennessee, Joseph Clark) 2 Idiotypes MCZ 178869.

fannyae Johnson, *Hyridella:* 1948, Nautilus, **62**, p. 47, pl. 3, fig. 1 (Marco River, Merauke, South Dutch New Guinea, P. T. L. Putnam) Holotype MCZ 160663.

feminalis Gould, *Anodon:* 1850, Pr. Boston Soc. Nat. Hist., **3**, p. 293; 1852 U. S. Expl. Exped., **12**, p. 436, fig. 547-547b (Wallawalla, Columbia River, Oregon, Dr. Pickering) 2 Cotypes MCZ 37294 ex Boston Soc. Nat. Hist.

ferrussaciana Lea, *Anodonta:* 1834, Tr. APS, **5**, p. 45, pl. 6, fig. 15; 1834, Obs., **1**, p. 157, pl. 6, fig. 15 (Ohio River, near Cincinnati, Ohio, T. G. Lea) 13 Paratypes MCZ 178770 ex T. G. Lea.

fimbriata Frierson, *Lampsilis:* 1907, Nautilus, **21**, p. 86, pl. 12, two upper figures and lower left hand one (Valles River, Mexico, A. A. Hinkley) 3 Cotypes MCZ 167699 from A. A. Hinkley ex B. Walker coll'n.

fisherianus Lea, *Unio:* 1838, Tr. APS, **6**, p. 8, pl. 4, fig. 8; 1838, Obs., **2**, p. 8, pl. 4, fig. 8 (Head of Chester River, Maryland, T. Fisher) 2 Idiotypes MCZ 178567.

flava Pilsbry and Bequaert, *Aspatharia:* 1927, Bull. Amer. Mus. Nat. Hist., **15**, p. 418, pl. 43, figs. 3-3a; pl. 44, figs. 2-2a (Medje, Belgian Congo, Lang and Chapin) 1 Paratype MCZ 142360. First published as a distinct species, Dr. Bequaert now regards this as a variety of *Aspatharia trapezia* v. Martens. "This form is close to typical *trapezia* and may prove to be only a synonym." (Bequaert)

flava Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1**, p. 160, pl. 14, fig. 3 (Michigan) Holotype MCZ 161866.

flavidens Benson, *Unio:* 1862, Ann. Mag. Nat. Hist., (3) **10**, p. 188; [was figured without name] 1862, Gleanings in Science, **1**, pl. 7, fig. 1 (Ganges River at Bhitoura, between Cawnpore and Allahabad [India]) 3 Paratypes MCZ 175559 ex W. H. Benson.

florentina Lea, *Unio:* 1857, PANSP, p. 83; 1862, Obs., **8**, p. 68, pl. 5, fig. 213 (Florence, Alabama, G. White; Cumberland River, Tennessee, Prof. Troost) 2 Idiotypes MCZ 178929.

flucki Walker, *Anodontites:* 1924, Nautilus, **38**, p. 53, pl. 1, figs. 3, 4 (Wanks River or Rio Coco, Nicaragua, W. H. Fluck) 3 Paratypes MCZ 167989 ex W. H. Fluck.

flucki Morrison, *Diplodon:* 1943, Nautilus, **57**, p. 14, pl. 5, fig. 5-9 (Orinoco River above Munduapo, Venezuela, W. H. Fluck) 4 Paratypes MCZ 167994 ex W. H. Fluck.

flucki Bartsch, *Nephronaias:* 1906, Pr. U. S. Nat. Mus., **30**, p. 393, pl. 27, figs. 2, 3, pl. 38, figs. 2, 3, pl. 39, figs. 1, 3 (Wounta River, north west of Kukallaya, Nicaragua, W. H. Fluck) 2 Paratypes MCZ 167491 ex W. H. Fluck.

folliculatus Lea, *Unio:* 1838, Tr. APS, **6**, p. 38, pl. 11, fig. 33; 1838, Obs., **2**, p. 38, pl. 11, fig. 33 (Savannah River [Georgia], Major Leconte) 1 Idiotype MCZ 178702 from South Carolina.

foremanianus Lea, *Unio:* 1842, Pr. APS, **2**, p. 224; 1842, Obs., **3**, p. 85, pl. 27, fig. 64 (Coosa River, Alabama, Dr. Brumby) 1 Idiotype MCZ 178753.

forsheyi Lea, *Unio:* 1859, PANSP, p. 155; 1859, Obs., **8**, p. 39, pl. 60, fig. 182 (Fayette County, Texas, Prof. Forshey; Alabama, J. G. Anthony) 8 Paratypes MCZ 178785 ex J. G. Anthony.

friersoni B. H. Wright, *Unio:* 1896, Nautilus, **9**, p. 134, pl. 3 (Bayou Pierre, an arm of the Red River in Desoto Parish, Louisiana) 5 Paratypes MCZ 165697 ex L. S. Frierson.

fryanus B. H. Wright, *Unio:* 1888, PANSP, p. 113, pl. 2, fig. 1 (Lake Ashby, Volusia County, Florida) 4 Paratypes MCZ 37202 from B. H. Wright, from the E. W. Roper coll'n. ex Boston Soc. Nat. Hist.

fucatus Lea, *Unio:* 1860, PANSP, p. 92; 1860, Obs., **8**, p. 35, pl. 59, fig. 178 (North Alabama, Prof. Tuomey; Tuscumbia [Alabama], L. B. Thornton) 1 Idiotype MCZ 178898, from Murfreesboro, Tennessee.

fulgidus Lea, *Unio:* 1845, PANSP, p. 164; 1848, Obs., **4**, p. 47, pl. 4, fig. 10 (Alexandria, Louisiana, J. Hale) 1 Idiotype MCZ 178784.

fuscatus Lea, *Unio:* 1843, Desc. 12 Uniones [no pagination]; 1848, Obs., **4**, p. 35, pl. 40, fig. 4 (Black Creek, Florida, S. B. Buckley) 3 Idiotypes MCZ 178725.

ganina Pilsbry, *Lampsilis metallica:* 1909 [1910], PANSP, p. 539, pl. 27, fig. 6 (Ganina River, 3 miles southwest of San Dieguito [Mexico], A. A. Hinkley) 15 Cotypes MCZ 189371 from A. A. Hinkley ex B. Walker coll'n.

gastonensis Lea, *Unio:* 1863, PANSP, p. 191; 1867, Obs., **11**, p. 24, pl. 6, fig. 18 (Mine Creek, Gaston County, North Carolina, C. M. Wheatley) 1 Paratype MCZ 178773 ex C. M. Wheatley.

generosus Gould, *Unio:* 1847, Pr. Boston Soc. Nat. Hist., **2**, p. 220 (Newville, Tavoy [Burmah], Mrs. Vinton) ½ Cotype MCZ 161900 from A. A. Gould ex J. G. Anthony coll'n.

geometricus Lea, *Unio:* 1832, Tr. APS, **5**, p. 38, pl. 4, fig. 10; 1834, Obs., **1**, p. 150, pl. 4, fig. 10 (Bayou Teche, Louisiana, W. M. Stewart) 2 Idiotypes MCZ 178697.

genthii Lea, *Unio:* 1857, PANSP, p. 85; 1862, Obs., **8**, p. 61, pl. 2, fig. 204 Catawba River, Gaston County, North Carolina, Dr. Genth and C. M. Wheatley; Deep River, Gulf, North Carolina, Prof. Emmons) 2 Paratypes MCZ 178895 ex C. M. Wheatley.

gesnerii Lea, *Anodonta:* 1858, PANSP, p. 139; 1859, Obs., **7**, p. 49, pl. 31, fig. 109 (Uphaupee [Uphapee] Creek, Macon County, Alabama, Wm. Gesner) 2 Paratypes MCZ 152882 ex Wm. Gesner; 1 Idiotype MCZ 152883.

gibber Lea, *Unio:* 1838, Tr. APS, **6**, p. 34, pl. 10, fig. 30; 1838, Obs., **2**, p. 35, pl. 10, fig. 30 (Caney Fork River, Tennessee, Prof. Troost) 3 Metatypes MCZ 178804.

gibbum Benson, *Anodonta:* 1855, Jour. Asiatic Soc. Bengal, **34**, p. 135; (Tangtse Kaing, China) 3 Cotypes MCZ 177314 from W. H. Benson ex C. B. Adams coll'n.

glaber Lea, *Unio:* 1838, Tr. APS, **6**, p. 34, pl. 10, fig. 29; 1838, Obs., **2**, p. 34, pl. 10, fig. 29 (Holston River, Tennessee, Prof. Troost) 4 Idiotypes MCZ 178907.

gladiolus Heude, *Unio:* 1877, Conch. Fleuv. Nanking, Part 2, pl. 16, fig. 35 (Rivières de Ning-Kouo-fou et de Kouang-te-tchéou; lac Tai [China]) 2 Idiotypes MCZ 167248 from Hia-in-fou, China ex Musée Heude.

glandulosa Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1**, p. 163, pl. 16, fig. 3 (Michigan) Holotype MCZ 161869.

gouldianus 'Ward' Jay, *Unio:* 1839, Jay's Catalogue (third edit.), p. 24 [*nomen nudum*] 1 Cotype MCZ 143238 ex Dr. Ward.

gracilentus Lea, *Unio:* 1857, PANSP, p. 85; 1862, Obs., **8**, p. 62, pl. 3, fig. 205 (Catawba River, Gaston County, North Carolina, C. M. Wheatley) 3 Idiotypes MCZ 178701.

gracilis Lea, *Anodonta:* 1850 [1851] Pr. Zool. Soc. London, p. 197; 1860, Obs., **7**, p. 57, pl. 34, fig. 119 (Dingle, Isle of Panay [Philippine Islands], H. Cuming) 2 Paratypes MCZ 175581 ex H. Cuming.

granulatus Lea, *Unio:* 1861, PANSP, p. 60; 1867, Obs., **11**, p. 52, pl. 16, fig. 46 (Big Prairie Creek, Alabama, E. R. Showalter) 1 Paratype MCZ 178915 ex E. R. Showalter; 2 Idiotypes MCZ 178896.

grateloupiana Gassies, *Anodonta:* 1849, Moll. Agenais, p. 193, pl. 2, figs. 13-15, pl. 3, figs. 1-3, pl. 4, fig. 2 (la Garonne dans les nasses tranquilles et à fond vaseux; commune à Beauregard avant les travaux du Canal, trouvée aussi au bas de Rouquet par M. Ailkes; à Boé, dans les nasses) 1 Cotype MCZ 175636 ex J. P. S. de Grateloupe.

gravidus Lea, *Unio:* 1856, PANSP, p. 93; 1857, Obs., **6**, p. 12, pl. 24, fig. 5 (Siam) 4 Idiotypes MCZ 175553.

gundlachi Dunker, *Unio:* 1858, Malakozoologische Blätter, **5**, p. 228 (in flumine Taco Taco dicto insulae Cubanae, J. Gundlach) 1 Cotype MCZ 94849 ex W. Dunker.

haglieri Frierson, *Unio:* (*Pleurobema*): 1900, Nautilus, **13**, p. 109, pl. 2 (North River, Alabama, near Tynes) 2 Cotypes MCZ 134119 ex B. Walker coll'n.

hallenbeckii Lea, *Anodonta:* 1858, PANSP, **2**, p. 139; 1859, Obs., **7**, p. 50, pl. 32, fig. 112 (Uphaupee [Uphapee] Creek, Macon County, Georgia, W. Gesner). This is an error and should read Macon County, Alabama. 1 Paratype MCZ 150174 ex W. Gesner with the label: "A rare new species. All I have are of the same imperfect character having been carried over land by negroes for forty miles."

hallenbeckii Lea, *Unio:* 1859, PANSP, p. 170; 1860, Obs., **8**, p. 10, pl. 51, fig. 154 (Flat Rock Creek and Four Mile Creek, near Columbus, Georgia, G. Hallenbeck and Bishop Elliott) 5 Idiotypes MCZ 178728.

hanleyanus Lea, *Unio:* 1852, Tr. APS, **10**, p. 279, pl. 23, fig. 37; 1852, Obs., **5**, p. 35, pl. 23, fig. 37 (Coosawattee River, Murray County, Georgia, Dr. Boykin) 4 Metatypes MCZ 178802.

harperi B. H. Wright, *Unio:* 1899, Nautilus, **13**, p. 6 (Altamaha, Suwannee and Flint Rivers) 4 Paratypes MCZ 186969 from Suwannee River, Florida, from B. H. Wright ex B. Walker coll'n.

hartii B. H. Wright, *Unio (Elliptio) webbianus:* 1934, Nautilus, **47**, p. 95, pl. 10, figs. 3-4 (Lake Consuelo, Citrus County, Florida, near Floral City) 2 Paratypes MCZ 95947 ex B. H. Wright.

hartmanianum Lea, *Unio:* 1860, PANSP, p. 370; 1862, Obs., **8**, p. 77, pl. 8, fig. 222 (Coosa River, Wetumpka, Alabama, E. R. Showalter) 2 Paratypes MCZ 178827 ex E. R. Showalter.

hartwrightii B. H. Wright, *Unio:* 1896, Nautilus, **9**, p. 121, pl. 2, figs. 4-6 (Lake Beresford, Florida) 2 Cotypes MCZ 167687 ex B. Walker coll'n.

haseмani Ortmann, *Diplodon:* 1921, Mem. Carnegie Mus. Pittsburgh, Pa., **8**, p. 478, pl. 34, figs. 1-4; [gills] pl. 47, fig. 5; [glochidium] text fig. 4a (p. 469) (Rio Guaporé, near Rio São Simao, Matto Grosso, Brazil, J. D. Haseman) 1 Cotype MCZ 47040 ex Carnegie Museum.

hazelhurstianus Lea, *Unio:* 1858, PANSP, p. 166; 1859, Obs., **7**, p. 29, pl. 26, fig. 92 (Satilla River, Camden County, Georgia, T. C. Downie) 3 Idiotypes MCZ 178724.

hebetatus Conrad, *Unio:* 1854, PANSP, **2**, p. 296, pl. 26, fig. 5 (Missouri) 1 Idiotype MCZ 178782.

hinkleyi B. H. Wright, *Unio:* 1886, PANSP, p. 117, pl. 4, fig. 3 (Lake Monroe, Florida) 1 Idiotype MCZ 30299.

hippopoeus Lea, *Unio:* 1845, Pr. APS, **4**, p. 163; 1848, Obs., **4**, p. 41, pl. 1, fig. 1 (Lake Erie, Dr. Budd) 1 Metatype MCZ 176968.

holmbergi Doello-Jurado, *Mycetopoda:* 1923, Anal. Mus. Nac. Hist. Nat. Buenos Aires, Argentina, **31**, p. 518, pl. 1 (Rio Santa Lucía, provincia de Corrientes, como a 35 kilómetros de su desembocadura en el Rio Paraná, S. Aquirre and J. W. Gez) 1 Paratype MCZ 111722 ex Museo Nacional de Historia Natural de Buenos Aires.

hopetonensis Lea, *Unio:* 1838, Tr. APS, **6**, p. 29, pl. 11, fig. 24; 1838, Obs., **2**, p. 29, pl. 9, fig. 24 ([Altamaha River] Hopeton, near Darien [Georgia] procured by Prof. Shepard from his friend J. H. Cowper [Couper]) 4 Paratypes MCZ 165691 ex J. H. Couper; 2 Paratypes MCZ 155567 ex Prof. Shepard.

hydianus Lea, *Unio:* 1838, Tr. APS, **6**, p. 14, pl. 6, fig. 14; 1838, Obs., **2**, p. 14, pl. 6, fig. 14 (Teche River Louisiana, W. M. Stewart; vicinity of New Orleans [Louisiana], Mr. Barabino) 5 Idiotypes MCZ 28263.

iheringi Clessen, *Anodonta:* 1882, Malakozoologische Blätter [n. s.], **5**, p. 191, pl. 4, fig. 5 (Taquara [Rio Grande do Sul] del mundo nova, Brasiliae) 1 Paratype MCZ 194094 from H. Von Ihering ex S. Putzeys coll'n.

iheringi B. H. Wright, *Unio:* 1898, Nautilus, **12,** p. 93; figured 1900, Simpson, PANSP, p. 79, pl. 4, fig. 5 (San Saba River, Menard County, Texas) 2 Paratypes MCZ 20152 ex L. S. Frierson.

imbricata Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1,** p. 159, pl. 14, fig. 1 (Camp Lake, Michigan) Holotype MCZ 161860.

implicata Say, *Anodonta:* 1829, New Harmony [Indiana] Disseminator, **2,** No. 22, p. 340 (Pond in Danvers, Massachusetts, Dr. T. W. Harris) Neoholotype MCZ 176769, selected by Johnson, 1946, Occ. Papers on Mollusks, **1,** p. 112, pl. 16, figs. 1, 2. The type locality was changed to the Agawam River (Outlet of Halfway Pond), Plymouth, Massachusetts.

impressa Anthony, *Alasmodon:* 1865, Amer. Jour. Conch., **1,** p. 157, pl. 12, fig. 4 (Tennessee) Holotype MCZ 150666.

incrassatus Lea, *Unio:* 1840, Pr. APS, **1,** p. 286; 1842 Obs., **3,** p. 55, pl. 16, fig. 34 (Chattahoochee River, near Columbus, Georgia, Dr. Boykin) 4 Metatypes MCZ 178771.

ineptus Lea, *Unio:* 1852, Tr. APS, **10,** p. 261, pl. 15, fig. 12; 1852, Obs., **5,** p. 17, pl. 15, fig. 12 (Abbeville District, South Carolina, J. P. Barratt) 2 Idiotypes MCZ 178694.

inflata Lea, *Symphynota:* 1831, Tr. APS, **4,** p. 99, pl. 14, fig. 28; 1834, Obs., **1,** p. 169, pl. 14, fig. 28 (Alabama River [Alabama], Judge Tait) 2 Idiotypes MCZ 178754.

inornata Anthony, *Anodon:* 1866, Amer. Jour. Conch., **2,** p. 145, pl. 7, fig. 1 (Slawson's Lake, Michigan) Holotype MCZ 161876.

inornatus Lea, *Unio:* 1856, PANSP, p. 93; 1857, Obs., **6,** p. 13, pl. 25, fig. 6 (Siam, S. R. House) 1 Idiotype MCZ 175554.

insolidus Lea, *Unio:* 1872, PANSP, p. 159; 1874, Obs., **13,** p. 44, pl. 13, fig. 37 (Abbeville District, South Carolina, Dr. Barratt; Fredericksburg, Virginia, Dr. Emmons; Irwin's Creek, Mecklenberg Co., North Carolina, C. M. Wheatley) 1 Paratype MCZ 189369 ex C. M. Wheatley.

inspecta Iredale, *Aparcthyria:* 1843, Australian Zoologist, **10,** p. 191, pl. 2 (Holmes Creek, 12 mi. N. E. of Darwin, No. Territory, Australia, M. M. Ward) 1 Paratype MCZ 196597 ex Australian Museum.

interruptus Lea, *Unio:* 1838, Tr. APS, **6,** p. 15, pl. 6, fig. 15; 1838, Obs., **2,** p. 15, pl. 6, fig. 15 (Harpeth River, Tennessee, Prof. Troost) 2 Paratypes MCZ 5477 from Prof. Troost ex R. E. Call coll'n. 1 Idiotype MCZ 178923.

interventus Lea, *Unio:* 1861, PANSP, p. 60; 1862, Obs., **8**, p. 88, pl. 11, fig. 233 (Cahawba River, Alabama, E. R. Showalter) 1 Paratype MCZ 178796 ex E. R. Showalter; 1 Idiotype MCZ 178790 from Tennessee.

iridella Pilsbry and Frierson, *Lampsilis:* 1907, Nautilus, **21**, pl. 12, [2 lower right-hand figures]; 1908, Nautilus, **22**, p. 81 (Valles, Mexico, A. A. Hinkley) 3 paratypes MCZ 100405 from A. A. Hinkley ex Mus. Nat. Hist., Univ. Illinois, Urbana, Ill.

iridineus Heude, *Mycetopus:* 1874, Conch, Fleuv. Nanking, Part 1, pl. 8, fig. 19 (les rivières de Tai-ping-fou et de Fou-tcheou-fou [China]) 1 Paratype MCZ 167108 ex Musée Heude.

irisans Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1**, p. 163, pl. 16, fig. 2 (Bostwick's Lake [Kent County] Michigan) Holotype MCZ 161870.

irwinensis Lea, *Unio:* 1872, PANSP, p. 159; 1874, Obs., **13**, p. 48, pl. 15, fig. 42 (Irwin's Creek, North Carolina, C. M. Wheatley) 4 Paratypes MCZ 178787 ex C. M. Wheatley.

jacksoni Marshall, *Diplodon:* 1928, Pr. U. S. Nat. Mus., **74**, p. 1, pl. 4, figs. 1-3 (Arcas, Province of Minas Geraes, Brazil, R. W. Jackson) 2 Paratypes MCZ 52367 ex R. W. Jackson.

javanus Lea, *Unio:* 1840, Pr. APS, **1**, p. 285; 1842, Obs., **3**, p. 58, pl. 18, fig. 36 (Java, Von dem Busch) 3 Idiotypes MCZ 175568.

jayensis Lea, *Unio:* 1838, Tr. APS, **6**, p. 28, pl. 9, fig. 23; 1838, Obs., **2**, p. 28, pl. 9, fig. 23 (Florida, J. C. Jay) ½ Metatype MCZ 178720.

jejunus Lea, *Unio:* 1838, Tr. APS, **6**, p. 9, pl. 4, fig. 9; 1838, Obs., **2**, p. 9, pl. 4, fig. 9 (Roanoke, also near Camden, South Carolina, Dr. Blanding) 2 Idiotypes MCZ 178719.

jetschini Westerlund, *Margaritana margaritifera:* 1890, Fauna Paläarctischen Region, Part 7, p. 185 (Oester-Schlesien [Juppel River] b. Weidenau [Austria], R. Jetschin) 2 Cotypes MCZ 183476 from R. Jetschin ex D. Thaanum coll'n.

jewettii Lea, *Unio:* 1867, PANSP, p. 81; 1869, Obs., **12**, p. 36, pl. 37, fig. 89 (Sink of Noonan's Lake, Florida, Col. E. Jewett) 2 Paratypes MCZ 178695 ex E. Jewett.

jonesi Vander Schalie, *Lampsilis:* 1934, Nautilus, **47**, p. 125, pl. 15 (Pea River, at Priston's Mill, Dale County, Alabama, J. A. Burke) 2 Paratypes MCZ 98802 ex Mus. Zool. Univ. Michigan, Ann Arbor, Mich.

keinerianus Lea, *Unio:* 1852, PANSP, p. 251; 1852, Obs., **5**, p. 37, pl. 23, fig. 40 (Coosawattee River, Murray County, Georgia, Dr. Boykin) 2 Idiotypes MCZ 178828.

kingii B. H. Wright, *Unio:* 1900, Nautilus, **13,** p. 138 (A branch of the Flint River, Baker County, Georgia) 2 Cotypes MCZ 20156 from B. H. Wright ex L. S. Frierson.

kirklandianus S. H. Wright, *Unio:* 1897, Nautilus, **10,** p. 136 (Ochlockonee River, Leon Co., Florida) 6 Paratypes MCZ 189802 and 186840 from B. H. Wright ex B. Walker coll'n.

kirtlandianus Lea, *Unio:* 1834, Tr. APS, **5.** p. 98, pl. 14, fig. 41; 1834, Obs., **1,** p. 210, pl. 14, fig. 41 (Mahoning, Ohio, J. P. Kirtland) 2 Idiotypes MCZ 178738.

kullethensis Lea, *Unio:* 1864, PANSP, p. 285; 1869, Obs., **12,** p. 11, pl. 29, fig. 65 (Near Mardin, in a stream from Kulleth falling into the Tigris River [Iraq], C. M. Wheatley) 1 Paratype MCZ 152884 ex C. M. Wheatley.

lamarckianus Lea, *Unio:* 1852, Tr. APS, **10,** p. 266, pl. 17, fig. 20; 1852, Obs., **5,** p. 22, pl. 17, fig. 20 (Caddo River, Arkansas, Prof. Powell; Washitta River, near the Hot Springs, Arkansas, Dr. Hale) 2 Idiotypes MCZ 84651.

lanamensis Frierson, *Quadrula:* 1901, Nautilus, **15,** p. 75, pl. 4 (Lanana and Banita Creeks, near Nacogdoches, Texas, Messrs. Askew, Strode, and Frierson) 1 Paratype MCZ 69757 ex Dr. Strode.

lanceolatus Lea, *Unio:* 1828, Tr. APS, **3,** p. 266, pl. 3, fig. 2; 1834, Obs., **1,** p. 8, pl. 3, fig. 2 (Tar River at Tarborough [North Carolina], I. Lea) 3 Idiotypes MCZ 178926.

langi Pilsbry and Bequaert, *Mutela:* 1927, Bull. Amer. Mus. Nat. Hist., **53,** p. 432, pl. 39, figs. 3, 3a-b (Zambi, in the bed of an arm of the Congo, Belgian Congo, Lang and Bequaert) 6 Paratypes MCZ 41068. "Is a synonym of *Mutela nilotica angustata* Sowerby." (Bequaert).

laosensis Lea, *Unio:* 1866, PANSP, **4,** p. 63, pl. 21, fig. 61; 1867, Obs., **11,** p. 67, pl. 21, fig. 61 (Laos Mountains, Cambodia, Mons. Mouhot, per H. Cuming) 2 Paratypes MCZ 53982 ex C. M. Wheatley. Lea refers to these specimens.

largilliertí Philippi, *Unio:* 1847, Zeit, für Mal., **4,** p. 94 (Yucatan [Mexico], Largilliert) Lectotype MCZ 155569, selected by Johnson, 1951, Nautilus, **64,** p. 79, pl. 5, fig. 2. The type locality was restricted to San Geronimo, Campeche, Mexico. From Largilliert ex C. B. Adams coll'n. 1 Paratype MCZ 184531.

lato-marginata Lea, *Anodonta:* 1834, Tr. APS, **5,** p. 76, pl. 12, fig. 34; 1834, Obs., **1,** p. 188, pl. 12, fig. 34 (River Paraná [Argentina], Dr. Burrough) 1 Idiotype MCZ 175657.

latus Lea, *Unio:* 1859, PANSP, p. 171; 1860, Obs., **8,** p. 16, pl. 53, fig. 159 (Savannah River, near Savannah, Georgia, G. White and Major Le Conte) 3 Idiotypes MCZ 150808.

lawi Lea, *Unio:* 1871 PANSP, p. 189; 1874, Obs., **13,** p. 12, pl. 2, fig. 4 (Tennessee River, Tuscumbia, Alabama, B. Pybas; Tennessee River, Dr. Edgar; Holston River, A. E. Law and Prof. Cope) 2 Paratypes MCZ 37300 from A. E. Law ex J. Lewis.

lecontianus Lea, *Unio:* 1838, Tr. APS, **6,** p. 40, pl. 12, fig. 35; 1838, Obs., **2,** p. 40, pl. 12, fig. 35 (Conoochee River, Georgia, Major Le Conte) 1 Idiotype MCZ 178731.

lehmanii S. H. Wright, *Unio:* 1897, Nautilus, **10,** p. 138; figured by Simpson 1900, PANSP, p. 80, pl. 4, fig. 9 (St. Mary's River, Florida) 8 Idiotypes MCZ 178711.

lenior Lea, *Unio:* see under *lenis.*

lenis Lea, *Unio:* 1840, Pr. APS, **1,** p. 286; preoccupied, changed to *lenior,* 1842, Obs., **3,** p. 42, pl. 12, fig. 18 (Stone's River, Tennessee, S. M. Edgar) 5 Idiotypes MCZ 178901.

leprosus Miles, *Unio:* 1861, Report on the Zoology of Michigan for 1859-60, Lansing, Michigan, p. 30 (Huron River, Livingston County, Michigan) 1 Cotype MCZ 151653 from M. Miles ex Peabody Museum, Salem, Mass.

lesleyi Lea, *Unio:* 1860, PANSP, p. 360; 1860, Obs., **8,** p. 34, pl. 58, fig. 177 (Kentucky, J. Lesley; [near Murfreesboro] Tennessee, J. G. Anthony) 3 Paratypes MCZ 178815 ex J. G. Anthony.

lesueurianus Lea, *Unio:* 1840, Pr. APS, **1,** p. 286; 1842, Obs., **3,** p. 33, pl. 8, fig. 6 (Cany Fork and Holston River, Tennessee, S. M. Edgar) "Two specimens only of this species were brought by Mr. Edgar" (Lea). 1 Paratype MCZ 5293 from Edgar to Troost ex R. E. Call coll'n.

lewisii Lea, *Anodonta:* 1857, PANSP, p. 84; 1862, Obs., **8,** p. 44, pl. 62, fig. 187 (Erie Canal and Mohawk River, Herkimer County, N. Y., James Lewis; Genesee River, below Rochester, N. Y., C. Dewey) 2 Paratypes MCZ 161904 ex J. Lewis.

lewisii Lea, *Unio:* 1861, PANSP, p. 40; 1862, Obs., **8,** p. 75, pl. 8, fig. 220 (Coosa River, Alabama, E. R. Showalter) 1 Paratype MCZ 178835 ex E. R. Showalter; 2 Idiotypes MCZ 178823.

lineata Heude, *Anodon:* 1879, Conch. Fleuv. Nanking, Part 5, pl. 36, fig. 70 (Ou-yuen-hien [China]) 1 Paratype MCZ 167247 ex Musée Heude.

lineatus Lea, *Unio:* 1840, PANSP, p. 287; 1842, Obs., **3,** p. 44, pl. 12, fig. 20 (Chattahoochee River, Columbus, Georgia, Dr. Boykin) 1 Idiotype MCZ 146976.

lobensis Frierson, *Parreysia:* 1913, Nautilus, **27**, p. 85, pl. 5 (Lobo River, Kamerun, Africa, George Schwab) Holotype MCZ 21164.

lucasi Deshayes, *Anodonta:* 1847, Hist. Nat. Moll. Algeria, pl. 108, figs. 1-2 (La Calle, Algeria) 3 Cotypes MCZ 150634 ex G. B. Deshayes.

lugens Drouet and Chaper, *Unio:* 1892, Mém. Soc. Zool. France, **5**, p. 147, pl. 5, figs. 1-3 (le Kapocas (Semitau) à Borneo) 2 Paratypes MCZ 174097 from Chaper ex S. Putzeys coll'n.

lugubris Lea, *Unio:* 1834, Tr. APS, **6**, p. 30, pl. 9, fig. 25; 1838, Obs., **2**, p. 30, pl. 9, fig. 25 (Hopeton, near Darien, Georgia, Prof. Shepard) 2 Paratypes MCZ 37044 from J. H. Couper who gave them to Prof Shepard, who, in turn, sent them to Lea for description, ex Boston Soc. Nat. Hist.; 2 Idiotypes MCZ 178712.

lutulentus Gould, *Unio:* 1850, Pr. Boston Soc. Nat. Hist., **3**, p. 295; 1852, U. S. Expl. Exped., **12**, p. 428, fig. 542 a-e (New Zealand, Drayton) 12 Paratypes MCZ 155765 from the Smithsonian Institution ex C. B. Adams coll'n.

lyonii Lea, *Unio:* 1865, PANSP, p. 89; 1869, Obs., **12**, p. 19, pl. 32, fig. 74 (East Tennessee, S. S. Lyon) 1 Idiotype MCZ 178814.

maeer Lea, *Unio:* 1857, PANSP, p. 86; 1863, Obs., **9**, p. 24, pl. 29, fig. 271 (Roanoke River, Weldon, North Carolina, Prof. Emmons) 1 Idiotype MCZ 150813.

maestus Lea, *Unio:* 1841, Pr. APS, **2**, p. 82; 1842, Obs., **3**, p. 82, pl. 26, fig. 60 (French Broad River, East Tennessee, Prof. Troost and S. M. Edgar) 3 Paratypes MCZ 5596 from Prof. Troost ex R. E. Call coll'n; 2 Idiotypes MCZ 178917.

marcens Benson, *Unio flavidens:* 1862, Ann. Mag. Nat. Hist., (3) **10**, p. 188; figured by Hanley and Theobald, 1876, Conch. Indica, p. 19, pl. 42, figs. 4-6 (Berhampooter River, Assam [India], Col. Jenkins) 1 Cotype MCZ 175550 ex W. H. Benson.

mardinensis Lea, *Unio:* 1864, PANSP, p. 286; 1869, Obs., **12**, p. 12, pl. 30, fig. 66 (near Mardin, in a stream falling into the Tigris River, Asia [Iraq], C. M. Wheatley) 2 Cotypes MCZ 152886 ex C. M. Wheatley.

martensi Ihering, *Castalina:* 1893, Archiv für Natur., **59**, p. 81, pl. 3, fig. 5 (Rio Camaquam, Rio Grande do Sol [Brazil]) 8 Paratypes MCZ 192368 from H. von Ihering ex S. Putzeys coll'n.

menielii Anthony, *Anodon:* 1866, Amer. Jour. Conch., **2**, p. 144, pl. 6, fig. 1 ([Sand Lake] Michigan) Holotype MCZ 150644.

mearnsi Simpson, *Lampsilis:* 1900, PANSP, p. 75, pl. 1, fig. 4 (vicinity of Fort Clarke, Kinney County, Texas, E. A. Mearns) 4 Paratypes MCZ 87962 ex E. A. Mearns.

medellinus Lea, *Unio:* 1830, Tr. APS, **6,** p. 39, pl. 12, fig. 34; 1838, Obs., **2,** p. 39, pl. 12, fig. 34 (River Medellin, near Vera Cruz [Mexico], Dr. Burrough) 2 Paratypes MCZ 178881 ex Dr. Burrough.

medius Lea, *Unio:* 1861, PANSP, p. 40; 1862, Obs., **8,** p. 82, pl. 10, fig. 227 (near Coosa River, Alabama, E. R. Showalter) 3 Paratypes MCZ 178822, mentioned by Lea as being in the J. G. Anthony coll'n.

menkianus Lea, *Unio:* 1836, Tr. APS, **5,** p. 76, pl. 19, fig. 59; 1838, Obs., **2,** p. 76, pl. 19, fig. 59 (Harpeth River, Tennessee, Prof. Troost) 2 Idiotypes MCZ 178908.

meredithii Lea, *Unio:* 1858, PANSP, p. 40; 1862, Obs., **8,** p. 69, pl. 5, fig. 214 (Tennessee River, Tuscumbia, Alabama, L. B. Thornton) 4 Paratypes MCZ 178807 ex L. B. Thornton; 2 Idiotypes MCZ 178803.

merus Lea, *Unio:* 1852, Tr. APS, **10,** p. 260, pl. 15, fig. 10; 1852, Obs., **5,** p. 16, pl. 15, fig. 10 (Abbeville District, South Carolina, J. P. Barratt) 2 Idiotypes MCZ 178768 from Georgia.

micans Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1,** p. 162, pl. 16, fig. 1 (Texas) Holotype MCZ 187290.

micans Lea, *Unio:* 1857, PANSP, p. 85; 1862, Obs., **8,** p. 63, pl. 3, fig. 207 (Catawba River, Gaston County, North Carolina, C. M. Wheatley and Dr. Genth; Deep River, Gulf, North Carolina, Prof. Emmons) 2 Idiotypes MCZ 178718.

micropterus Morelet, *Unio:* 1866, Jour. de Conch., **14,** p. 63; 1875, Series Conchyliologique, Part 4, p. 349, pl. 15, fig. 6 (rivière Battambang, Cambodje [Cambodia], M. Le Mesle) 3 Paratypes MCZ 17045 ex A. Morelet.

mitchelli Simpson, *Unio:* 1896 [*in* Dall] Pr. U. S. Nat. Mus., **18,** p. 5; 1896, *ibid.* **19,** p. 371, pl. 32, figs. 1-3 (Guadaloupe River, Victoria County, Texas, J. D. Mitchell) 2 Paratypes MCZ 165695 from J. D. Mitchell ex Boston Soc. Nat. Hist.

mooresianus Lea, *Unio:* 1857, PANSP, p. 83; 1867, Obs., **11,** p. 43, pl. 114, fig. 37 (Tuscumbia, Alabama, L. B. Thornton) 2 Paratypes MCZ 25621 from Thornton ex R. E. Call coll'n.; 2 Idiotypes MCZ 178795 from Tennessee.

moreletianus Heude, *Unio:* 1877, Conch. Fleuv. Nanking, Part 8, pl. 60, fig. 117 (La rivière de Konang-té-tcheou [China]) 1 Paratype MCZ 167115 ex Musée Heude.

mosulensis Lea, *Unio:* 1863, PANSP, p. 190; 1867, Obs., **11**, p. 56, pl. 17, fig. 49 (River Tigris at Mosul [Iraq], C. M. Wheatley) 2 Paratypes MCZ 161976 ex C. M. Wheatley.

mucidus Morelet, *Unio:* 1845, Moll. du Portugal, p. 111, pl. 14, fig. 3 (rivières du nord et notamment dans la Taméga, le Cavado et la Lima [Portugal]) 2 Paratypes MCZ 152880 ex A. Morelet.

mundus Lea, *Unio:* 1857, PANSP, p. 83; 1867, Obs., **11**, p. 44, pl. 14, fig. 38 (Tuscumbia, Alabama, L. B. Thornton) 5 Idiotypes MCZ 178805.

murchisonianus Lea, *Unio:* 1834, Tr. APS, **5**, p. 33, pl. 3, fig. 6; 1834, Obs., **1**, p. 145, pl. 3, fig. 6 (China, Mrs. Murchison) 4 Idiotypes MCZ 175569 from India.

nankingensis Heude, *Monocondylaea:* 1874, Jour. de Conch., **22**, p. 116; 1875, Conch. Fleuv. Nanking, Part 1, pl. 4, fig. 9 (rivière de Nanking [China]) 2½ Paratypes MCZ 167240 ex Musée Heude.

napeanensis Conrad, *Unio:* 1852, PANSP, p. 10; 1854, JANSP, **2**, p. 296, pl. 26, fig. 3 ([Nepean River, New South Wales, Australia]) 1 Paratype MCZ 72077 from T. A. Conrad ex Acad. Nat. Sci. Philadelphia.

nashvillianus Lea, *Unio:* 1834, Tr. APS, **5**, p. 100, pl. 14, fig. 43; 1834, Obs., **1**, p. 212, pl. 14, fig. 43 (Cumberland River [Tennessee], Prof. Troost; Ohio [River] at Louisville [Kentucky], Dr. Fitch) 2 Paratypes MCZ 16380 from Prof. Troost ex R. E. Call coll'n; 3 Idiotypes MCZ 178902.

negatus Lea, *Unio:* 1861, PANSP, p. 59; Obs., **8**, p. 80, pl. 9, fig. 225 (Big Prairie Creek, Alabama, E. R. Showalter; Columbus, Mississippi, W. Spillman) 4 Paratypes MCZ 130562 ex E. R. Showalter; 2 Paratypes MCZ 5665 ex W. Spillman; 2 Idiotypes MCZ 178776 from Alabama.

neislerii Lea, *Unio:* 1858, PANSP, p. 165; 1859, Obs., **7**, p. 30, pl. 26, fig. 93 (Flint River at Lanier, Georgia, H. M. Neisler; at Macon [County] Georgia, J. C. Plant) 2 Paratypes MCZ 189796 ex H. M. Neisler.

Lanier was about 10 miles north of Oglethorpe, Macon County, Georgia. It does not appear on modern maps. It is not to be confused with the town of the same name in Bryan County. Both of the type lots probably came from the same source.

nicaraguae Philippi, *Anodonta:* 1848, Zeit. für Mal., **5**, p. 130 (Nicaragua, Largilliert) 1 Paratype MCZ 184530 from Largilliert ex C. B. Adams was selected by Johnson (1951, Nautilus, **64**, p. 81, pl. 5, fig. 1) as lectotype. This selection was, however, invalid as a lectotype for this species had been previously selected by Haas (1930, Senckenbergiana, **12**, p. 322, fig. 1); see, Johnson (1951, Nautilus, **65**, p. 32); also 1 Paratype MCZ 17071 from Largilliert ex J. G. Anthony.

nitens Lea, *Unio:* 1840, Pr. APS, **1.** p. 288; 1842, Obs., **3.** p. 43, pl. 12, fig. 19 (Long Creek, Cocke County, Tennessee, S. M. Edgar) 3 Paratypes MCZ 5666, mentioned by Lea as being in the G. Troost coll'n., ex R. E. Call coll'n.

notatus Lea, *Unio:* 1838, Tr. APS, **6.** p. 28, pl. 8, fig. 22; 1838, Obs., **2.** p. 28, pl. 8, fig. 22 (Cumberland River [Tennessee], Prof. Troost) 1 Idiotype MCZ 178911.

nubilus Lea, *Unio:* 1868, PANSP, p. 161; 1869, Obs., **12.** p. 58, pl. 44, fig. 110 (Paw Creek, Menklenburg County, North Carolina, C. M. Wheatley) 1 Paratype MCZ 178730 ex C. M. Wheatley.

nux Lea, *Unio:* 1852, Tr. APS, **10.** p. 283, pl. 24, fig. 43; 1852, Obs., **5.** p. 39, pl. 24, fig. 43 (Alabama River [Alabama], C. M. Wheatley) 3 Idiotypes MCZ 178794.

nyangensis Frierson, *Parreysia:* 1913, Nautilus, **27.** p. 86, pl. 5 (Nyang River, Kamerun, Africa, George Schwab) Holotype MCZ 21160.

obesa Connolly, *Cafferia caffra:* 1925, Records Albany [South Africa] Mus., **3.** p. 263, pl. 11, figs. 1-4 (Bushman's River, Alicedale, Cape Province [Union of South Africa]) 4 Paratypes MCZ 52457 from M. Connolly.

obesus Lea, *Unio:* 1831, Tr. APS, **4.** p. 96, pl. 113, fig. 26; 1834, Obs., **1.** p. 106, pl. 113, fig. 26 (York River, Virginia, [Georgia, teste Lea, Obs., **1.** p. 118] W. Cooper) 2 Paratypes MCZ 165693, from W. Cooper ex Boston Soc. Nat. Hist.; 1 Idiotype MCZ 178698 from Prairie Creek, Florida.

oblatus [*sic*] Lea, *Unio:* see under *albatus.*

obtusus Lea, *Unio:* 1840, Pr. APS, **1.** p. 287; 1842, Obs., **3.** p. 39, pl. 11, fig. 13 (Chattahoochee River, Columbus, Georgia, Dr. Boykin) 3 Idiotypes MCZ 146980.

occultus Lea, *Unio:* 1843, Des. 12 Uniones [no pagination]; 1848, Obs., **4.** p. 37, pl. 41, fig. 7 (Black Creek and Lake Monroe, Florida, S. B. Buckley) 2 Idiotypes MCZ 178916.

ochracea Say, *Unio:* 1817, Nicholson's Encyclopedia, **2.** [no pagination], pl. 3, fig. 8 (Delaware and Schuylkill Rivers [Pennsylvania]) Neoholotype MCZ 178838 selected by Johnson (1947, Occ. Papers on Mollusks, **1.** p. 153, pl. 20, fig. 2). The type locality was restricted to the Schuylkill River, near Philadelphia, Pa.

ogeecheensis Conrad, *Unio:* 1849, PANSP, p. 153; 1850, JANSP, **1.** p. 275, pl. 37, figs. 3-4 ([Ogeechee River, Georgia], J. H. Couper) Lectotype, here selected, MCZ 146971 is the specimen from which figure 3 was drawn ex J. H. Couper.

oleivorus Heude, *Mycetopus:* 1877, Conch. Fleuv. Nanking, Part 3, pl. 22, fig. 46 (La Hoai supériere, département de Ing-teh'eou [China]) 2 Paratypes MCZ 167110 ex Musée Heude.

opalina Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1**, p. 159, pl. 14, fig. 2 (Shear's Lake [Kent County] Michigan) Holotype MCZ 150633.

opalinus Anthony, *Unio:* 1866, Amer. Jour. Conch., **2**, p. 146, pl. 7, fig. 2 (Michigan) Holotype MCZ 161893.

orinocensis Morrison, *Castalia:* 1943, Nautilus, **57**, p. 14, pl. 5, figs. 1-4 (Orinoco River at Maipures, U. S. Colombia, W. H. Fluck) 2 Paratypes MCZ 167992 ex W. H. Fluck.

orphaensis Lea, *Unio:* 1864, PANSP, p. 285; 1869, Obs., **12**, p. 10, pl. 29, fig. 64 (Tigris River, near Mardin, Pashalic of Orpha, Asiatic Turkey [Iraq], C. M. Wheatley) 3 Paratypes MCZ 152885 ex C. M. Wheatley.

ortmanni Walker, *Micromya:* 1925, Occ. Papers Mus. Zool., Univ. Michigan, No. 163, p. 1, pl. 1, figs. 1-6 (Green River, Mammoth Cave. Also Sulphur Fork of Russell Creek, Adair County, Kentucky) Holotype MCZ 167705; Allotype MCZ 167702; 1 Paratype MCZ 167703 all from the former locality.

ortmanni Pilsbry and Bequaert, *Pseudospatha:* 1927, Bull. Amer. Mus. Nat. Hist., **53**, p. 446, pl. 45, figs. 5, 7 (Lake Tanganyika: Bay of Toa in 5 m.; Tembwe; Moliro [Belgian Congo]) 1 Paratype MCZ 41070 from Tembwe. "Is a variety of *Pseudospatha tanganyicensis* Smith." (Bequaert).

ortmanni Frierson, *Unio* (*Nephronaias*)*:* 1913, Nautilus, **27**, p. 14, pl. 2 (Conchin's River, near Quirigua, Guatemala, Atlantic Drainage, A. A. Hinkley) 3 Cotypes MCZ 20916 ex A. A. Hinkley.

osbecki Philippi, *Unio:* 1845, Zeit, für Mal. **1**, p. 164; 1847, Abbild. und Beschr. Conch., **3**, p. 45, pl. 3, fig. 1 (Yang-tse-kiang, China, Largilliert) 2 Paratypes MCZ 187289 ex Largilliert.

oscari B. H. Wright, *Unio:* 1892, Nautilus, **5**, p. 124; 1896, Nautilus, **9**, p. 122, pl. 2, figs. 1-3 (A creek near Lake Osceola, at Winter Park, Florida) 15 Cotypes MCZ 178717 ex B. H. Wright.

ovata Simpson, *Quadrula:* see under *vestitus* Heude, *Unio:*

ozarkensis Call, *Unio:* 1887, Pr. U. S. Nat. Mus., **10**, p. 498, pl. 27 (Currant River, Shannon County, Missouri, and in Jack's Fork and Big Creek, tributaries to it) Holotype MCZ 5707; Allotype MCZ 5705 both from Jack's Fork, ex R. E. Call coll'n.

pallaryi Longstaff, *Nodularia teretiscula* var: 1914, Jour. Linn. Soc. London, Zool., **32**, p. 256 (near Mogran, Anglo-Egyptian Sudan [Also listed from a dozen nearby localities], J. Longstaff) 1 Paratype MCZ 173051 ex T. Pain.

pallida Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1**, p. 162, pl. 15, fig. 3 (Michigan) Holotype MCZ 161871.

paludicolus Gould, *Unio:* 1845, Pr. Boston Soc. Nat. Hist., **2**, p. 53 (Everglades of Florida, J. Bartlett) 1 Idiotype MCZ 178705.

panacoensis Von dem Busch, *Unio:* 1843, [*in* Philippi] Abbild. und Beschr. Conch., **1**, p. 75, pl. 2 (Flumea Panaco, prope Tampico, Mexico) 3 Paratypes MCZ 178882 ex Von dem Busch.

papyracea Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1**, p. 161, pl. 15, fig. 2 (locality unknown [Potomac River, Virginia]) Holotype MCZ 150656.

paramattensis Lea, *Unio:* 1862, PANSP, p. 176; 1867, Obs., **11**, p. 64, pl. 20, fig. 59 (Paramatta River, New South Wales, Smithsonian Institution) ½ Paratype MCZ 17015 ex Smithsonian Institution.

parcedentata Haas, *Nodularia:* 1911, Nach. Deutschen Mal. Ges., **43**, p. 43; 1911, Conch, Cab., **9**, Part 2, Section 2, p. 104, pl. 12a, figs. 3-4. (Mikawa, Japan, Hirase) 1 Paratype MCZ 44650 ex S. Hirase.

parvulus Heude, *Unio:* 1878, Conch. Fleuv. Nanking, Part 4, pl. 32, fig. 65 (Petits ruisseaux souvent à sec, qui reçoivent les eaux des rizières dans les vallons du Kien-té sud (Ngan-houé) [China]) 1½ Paratypes MCZ 167246 ex Musée Heude.

patsaligensis Simpson, *Pleurobema:* 1900, PANSP, p. 82, pl. 2, fig. 1; (Little Patsaliga, southeast Alabama) 2 Paratypes MCZ 20179 ex L. S. Frierson; 2 Paratypes MCZ 210276 ex B. Walker coll'n.

paulus Lea, *Unio:* 1840, Pr. APS, **1**, p. 287; 1842, Obs., **3**, p. 51, pl. 15, fig. 29 (Chattahoochee River, Columbus, Georgia, Dr. Boykin) 3 Idiotypes MCZ 178892.

peguensis Anthony, *Monocondyloea* [*sic*]*:* 1865, Amer. Jour. Conch., **1**, p. 205, pl. 18, fig. 2 (Pegu, British Burma) Holotype MCZ 161877; 22 Paratypes MCZ 161874.

peguensis Anthony, *Unio:* 1865, Amer. Jour. Conch., **1**, p. 351, pl. 25, fig. 2 (Pegu, British Burma) Holotype MCZ 161875; 1 Paratype MCZ 161876.

pellis-lacerti Morelet, *Unio:* 1865, Jour. de Conch., **13**, p. 22; 1875, Series Conchologique, Part 4, p. 355, pl. 17, fig. 5 (Siam) 3 Paratypes MCZ 175551 ex A. Morelet.

penicillatus Lea, *Unio:* 1857, PANSP, p. 171; 1859, Obs., **7.** p. 21, pl. 23, fig. 85 (Chattahoochee [River] near Columbus, Georgia, Dr. Boykin; near Atlanta [Georgia], Bishop Elliott; Flint River, near Albany, Georgia, Bishop Elliott and G. White) 3 Idiotypes MCZ 178930.

percoarctatus Lea, *Unio:* 1857, PANSP, p. 85; 1862, Obs., **8.** p. 63, pl. 3, fig. 206 (Catawba River, Gaston County, North Carolina, C. M. Wheatley and Dr. Genth) 3 Idiotypes MCZ 152239.

pernodosus Lea, *Unio:* 1845, Pr. APS, **4.** p. 163; 1848, Obs., **4.** p. 45, pl. 3, fig. 8 (North Carolina, W. B. Budd) 2 Idiotypes MCZ 178831.

personatus Say, *Unio:* 1829, New Harmony [Indiana] Disseminator, **2.** No. 20, p. 309 (Wabash River [Indiana]) 4 Idiotypes MCZ 25763 from the Cumberland River, Tennessee. Named by Say (see Call, 1898, Mollusca of Indiana, p. 475), from G. Troost ex R. E. Call coll'n.

perstriatus Lea, *Unio:* 1852, Tr. APS, **10.** p. 255, pl. 12, fig. 3; 1852, Obs., **5.** p. 11, pl. 12, fig. 3 (Abbeville District, South Carolina, Dr. Barratt) 3 Idiotypes MCZ 178691.

pictus Lea, *Unio:* 1834, Tr. APS, **5.** p. 73, pl. 11, fig. 32; 1834, Obs., **1.** p. 185, pl. 11, fig. 32 (Harpeth River, Tennessee, Prof. Troost). Figured Holotype MCZ 5792 from G. Troost ex R. E. Call coll'n; 1 Idiotype MCZ 146977.

pilaris Lea, *Unio:* 1840, Pr. APS, **1.** p. 285; 1842, Obs., **3.** p. 47, pl. 14, fig. 24 (French Broad and Holston Rivers, East Tennessee, S. M. Edgar) 1 Paratype MCZ 5783 from the French Broad River, mentioned by Lea as being in the Troost coll'n., ex R. E. Call coll'n.; 3 Idiotypes MCZ 178780.

pinei B. H. Wright, *Unio:* 1897, Nautilus, **11.** p. 40; figured by Simpson, 1900, PANSP, p. 80, pl. 3, fig. 1 (An unnamed lake in Withlacoochee River Region of Hernando County, Florida) 2 Paratypes MCZ 20153 ex L. S. Frierson.

pinkstonii B. H. Wright, *Unio:* 1897, Nautilus, **10.** p. 136 (Tuscaloosa [Tallapoosa] River, Macon County, Alabama) 2 Cotypes MCZ 189647 ex B. Walker coll'n.

planilaterus Conrad, *Unio:* 1838, Monography Family Unionidae, Part 12, p. 103, pl. 57, fig. 1 (Black Water River, Virginia; Neuse River, North Carolina; Yadkin River, North Carolina, Dr. Blanding) 2 Idiotypes MCZ 124885 from Louisiana.

pleasii Marsh, *Unio:* 1891, Nautilus, **5.** p. 2 (Little Red River, Arkansas) 5 Idiotypes MCZ 29988.

plebeius Adams, *Unio compressus:* 1842, Thompson's History of Vermont, Part 1, p. 166 (Middlebury [Vermont]). There were four specimens in the original lot. The largest one, whose measurements are given in the original description is here selected as Lectotype MCZ 154361; 3 Paratypes MCZ 154366 ex C. B. Adams coll'n.

plectophorus Conrad, *Unio:* 1849, PANSP, p. 162 [as *plectrophorus*]; 1850, JANSP, **1**, p. 277, pl. 38, fig. 7 (Flint River, Georgia, J. H. Couper) 3 Paratypes MCZ 178840 and 28339 ex J. H. Couper.

pliciferus Lea, *Unio:* 1838, Tr. APS, **5**, p. 61, pl. 17, fig. 53; 1838, Obs., **2**, p. 61, pl. 17, fig. 53 (Mexico, Dr. Burrough) 7 Idiotypes MCZ 6584.

polymorphus B. H. Wright, *Unio:* 1899, Nautilus, **13**, p. 42 (Spanish Creek, Okefenokee Swamp, Charlton County, Georgia) 5 Cotypes MCZ 30290 ex B. Walker coll'n.

polystictus Heude, *Unio:* 1877, Conch. Fleuv. Nanking, Part 2, pl. 12, fig. 25 (riviére Siang [Hounan Province, China]) 1 Paratype MCZ 167116 ex Musée Heude.

popenoi Call, *Unio:* 1885, Bull. Washburn College, **1**, p. 49, pl. 2 (Fall River, Wilson County, Kansas; Verdigris River, Kansas) Holotype MCZ 4934 from the former locality ex R. E. Call coll'n.

postellii Lea, *Unio:* 1858, PANSP, p. 165; 1859, Obs., **7**, p. 32, pl. 26, fig. 94 (Randall's Creek, near Columbus, Georgia, Bishop Elliott; Carter's Creek, Baldwin County, Georgia, Mr. Postell) 5 Idiotypes MCZ 124883.

powellii Lea, *Unio:* 1852, Pr. APS, **5**, p. 252; 1852, Obs., **5**, p. 26, pl. 19, fig. 25 (Saline River, Arkansas, Prof. Powell) 1 Paratype MCZ 178884 ex Prof. Powell.

prattii Lea, *Unio:* 1858, PANSP, p. 166; 1859, Obs., **7**, p. 24, pl. 24, figs. 88, 88a (Chattahoochee River at Roswell, Cobb County, Georgia, N. A. Pratt, Jr. and J. Postell) 1 Idiotype MCZ 146989.

productus Conrad, *Unio:* 1836, Monography Family Unionidae, Part 3, p. 31, pl. 14, fig. 1 (Savannah River at Augusta [Georgia], M. Phillips) 3 Idiotypes MCZ 178692 from the Shenandoah River, Jefferson County, West Virginia ex Dr. W. D. Hartmann.

propinquus Lea, *Unio:* 1857, PANSP, p. 88; 1862, Obs., **8**, p. 67, pl. 5, fig. 212 (Florence, Alabama, G. White; Tuscumbia, Alabama, L. B. Thornton) 4 Paratypes MCZ 178566 ex L. B. Thornton.

proximus Lea, *Unio:* 1852, Pr. APS, **5**, p. 252; 1852, Obs., **5**, p. 27, pl. 20, fig. 27 (Georgia, J. P. Barratt) 2 Idiotypes MCZ 146981.

pugio, Benson, *Unio:* 1862, Ann. Mag. Nat. Hist., (3) **10,** p. 193; 1870, Hanley and Theobold, Conch. Indica, p. 5, pl. 19, fig. 7 (In regione Ava [Burma], W. Theobold) Theobold sent only one worn right valve of this species to Benson for description. Our specimens are from Theobold's original lot. 3 Paratypes MCZ 175560 ex W. Theobold.

pulcher Lea, *Unio:* 1838, Tr. APS, **6,** p. 6, pl. 3, fig. 6; 1838, Obs., **2,** p. 6, pl. 3, fig. 6 (near Nashville, Tennessee, Prof. Troost) Prof. Troost lent Lea one specimen of this species for description. We have Troost's original lot with the label, "*U. pulcher* Lea, Harpeth River, Tennessee. Mr. Lea has I think improperly made from the varieties of this two other species" (presumably *U. menkianus* and *U. interruptus*). We are unable to tell which specimen was the one figured. 6 Cotypes MCZ 5824 ex R. E. Call coll'n.

pullatus Lea, *Unio:* 1856, PANSP, p. 262; 1858, Obs., **6,** p. 57, pl. 8, fig. 39 (Creeks near Columbus, Georgia, Bishop Elliott) 1 Idiotype MCZ 178715.

pulvinulus Lea, *Unio:* 1845, Pr. APS, **4,** p. 164; 1848, Obs., **4,** p. 55, pl. 8, fig. 24 (Tuscaloosa and Coosawattee River, Murray County, Alabama, B. W. Budd) 3 Idiotypes MCZ 178820.

punctatus Lea, *Unio:* 1865, PANSP, p. 89; 1869, Obs., **12,** p. 21, pl. 32, fig. 76 (Caney Fork, Tennessee, S. M. Edgar; Tuscumbia, Alabama, B. Pybas) 1 Idiotype MCZ 178897 from Tennessee.

pusilla Simpson, *Quadrula granifera:* 1900, Pr. U. S. Nat. Mus., **22,** p. 795 (Green River, at Mammoth Cave, Kentucky) Lectotype, here selected, MCZ 20176, Pl. 2, fig. 4. This is the first time that this species has been figured. Ex L. S. Frierson.

pusillus Lea, *Unio:* 1840, PANSP, p. 286; 1842, Obs., **3,** p. 58, pl. 18, fig. 36 (Ogechee [Ogeechee] River, Georgia, Major Le Conte) 2 Idiotypes MCZ 178766.

pybasii Lea, *Unio:* 1858, PANSP, p. 40; 1862, Obs., **8,** p. 71, pl. 6, fig. 216 (Tennessee River, Tuscumbia, Alabama, B. Pybas) 3 Idiotypes MCZ 178904.

pyriformis Lea, *Unio:* 1857, PANSP, p. 31; 1858, Obs., **6,** p. 69, pl. 12, fig. 50 (near Columbus, Georgia, Bishop Elliott) 2 Idiotypes MCZ 178808.

radians Lea, *Unio:* 1857, p. 32; 1859, Obs., **7,** p. 19, pl. 23, fig. 84 (Othcalooga Creek, Gordon County, Georgia, Bishop Elliott) 1 Idiotype MCZ 178906.

radulosus Drouet and Chaper, *Unio:* 1892, Mém. Soc. Zool. France, **5,** p. 150, pl. 5, figs. 10-12 (le Sebroeang à Bornéo) 2 Paratypes MCZ 174096 ex S. Putzeys coll'n.

raccnsis Lea, *Unio:* 1859, PANSP, p. 171; 1860, Obs., **8,** p. 13, pl. 52, fig. 156 (Chattahoochee [River] near Columbus and Rae's Creek, Georgia, Bishop Elliott) 2 Idiotypes MCZ 124881.

ravenelianus Lea, *Unio:* 1834, Tr. APS, **5,** p. 32, pl. 3, fig. 5; 1834, Obs., **1,** p. 144, pl. 3, fig. 5 (French Broad River, tributary to the Tennessee, near Asheville, North Carolina, Prof. Ravenel) 2 Idiotypes MCZ 178806 from Alabama.

ravistellus Morelet, *Unio:* 1849, Testacea Novissima Insulae Cubanae, **1,** p. 29 (in Lacu Yzabal, reipublicae Guatemalensis) 1 Idiotype MCZ 178706.

reclusus B. H. Wright, *Unio:* 1898, Nautilus, **11,** p. 111 (Ocklocknee [Ochloeknee] River, Leon Co., Florida) 25 Paratypes MCZ 167685 from B. H. Wright ex B. Walker coll'n.

reeveianus Lea, *Unio:* 1852, Tr. APS, **10,** p. 272, pl. 20, fig. 28; 1852, Obs., **5,** p. 28, pl. 20, fig. 28 (Alexandria, Louisiana, J. Hale and Prof. Powell) 1 Paratype MCZ 178918 ex Prof. Powell with the label "*U. Reeveianus* Lea, Arkansas [*sic*] Lea so decided from this specimen and another," 2 Idiotypes MCZ 178879.

resupinatus Von Martens, *Pseudodon:* 1902, Nach. Deutsch. Mal. Gesell., **34,** p. 131 (Than-Moi, Tonkin [French Indo-China], Fruhstorfer) Lectotype MCZ 167691 selected by Johnson, 1948, Nautilus, **62,** p. 50, pl. 3, fig. 3; ½ Paratype MCZ 167672 ex B. Walker coll'n. For a discussion of this type designation see: Baker, H. B. 1950, Nautilus, **63,** p. 128; Johnson, R. I., 1950, Nautilus, **63,** p. 125; Zilch, A., 1950, Archiv für Molluskenkunde, **79,** p. 87.

rhombica Anthony, *Alasmidon:* 1865, Amer. Jour. Conch., **1,** p. 158, pl. 12, fig. 5 (Michigan) Holotype MCZ 50296.

richardsoni Von Martens, *Anodonta:* 1900, Biologia Centrali Americana, Moll., p. 529, pl. 41, figs. 1, 1a, 2, 2a (Rio Ameca, state of Jalisco, Mexico, Richardson), 3 Cotypes MCZ 6808 ex F. D. Godman.

riograndensis Von Ihering, *Anodonta:* 1890, Arch. Naturgesch., **1,** p. 154, (Rio Grande do Sul, Brazil) 3 Cotypes MCZ 192370 ex S. Putzeys coll'n.

rosaceus Conrad, *Unio:* 1850, JANSP, **1,** p. 275, pl. 37, fig. 5 (Savannah River [Georgia], J. H. Couper) Holotype MCZ 178779 ex J. H. Couper.

rosea Heude, *Anodon:* 1881, Conch. Fleuv. Nanking, Part 7, pl. 50, fig. 93 (les environs de Fou-tcheou (Fou-kien) [China]) ½ Paratype MCZ 167249 ex Musée Heude.

rostrum Lea, *Unio:* 1861, PANSP, p. 391; 1863, Obs., **9.** p. 23, pl. 29, fig. 270 (Davidson County, North Carolina, Dr. Genth) 1 Idiotype MCZ 178698.

rotula Pilsbry and Bequaert, *Caelatura* (*Laevirostris* ?): 1927, Bull. Amer. Mus. Nat. Hist., **53.** p. 405, pl. 33, figs. 5-5a (Congo River at Leopoldville [Belgian Congo]) 2 Paratypes MCZ 86183. "Is a synonym of *Caelatura* (*Laevirostris*) *bourguignati* de Rochebrune." (Bequaert).

rugatus Menke, *Unio:* 1828, Synopsis Molluscorum, p. 90 (In Germaniae rivis; in principatus Pyrmontani fluvio Emmer, in principatus Schaumburgo-Lippiaci rivo Aue, et in rivo Aue prope Hildesiam) 1 Cotype MCZ 152876 from Germany, from C. Menke ex W. Dunker.

rutilans Lea, *Unio:* 1856, PANSP, p. 262; 1858, Obs., **6.** p. 59, pl. 9, fig. 41 (Othcalooga Creek, Gordon County, and Columbus, Georgia, Bishop Elliott) 3 Metatypes MCZ 178933 from Columbus, Georgia.

saccellus Drouet and Chaper, *Unio:* 1892, Mém. Soc. Zool. France, **5.** p. 148, pl. 5, figs. 4-6 (le Sebroeang à Borneo) 1 Paratype MCZ 174095 from Chaper ex S. Putzeys coll'n.

sacculus Anthony, *Unio:* 1865, Amer. Jour. Conch., **1.** p. 157, pl. 12, fig. 3 (Tennessee) Holotype MCZ 161898.

sagittiformis Lea, *Unio:* 1852, Tr. APS., **10.** p. 277, pl. 22, fig. 35; 1852, Obs., **5.** p. 33, pl. 22, fig. 35 (Oconee River, near Athens, Georgia, Major Le Conte) 8 Idiotypes MCZ 178687.

salebrosus Lea, *Unio:* 1859, PANSP, p. 170; 1860, Obs., **8.** p. 14, pl. 52, fig. 157 (Flat Rock Creek [and] Bull Creek [Georgia], G. Hallenbeck; Chattahoochee River, near Columbus, Georgia, Bishop Elliott) 3 Idiotypes MCZ 150812.

sanctorumjohanium B. H. Wright, *Unio* (*Elliptio*): 1933, Nautilus, **47.** p. 17, pl. 1 (Lake Druid, near Floral City, Florida) 2 Paratypes MCZ 81972 ex B. H. Wright.

satur Lea, *Unio:* 1852, Pr. APS., **10.** p. 252; 1852, Obs., **5.** p. 21, pl. 17, fig. 19 (Alexandria, Louisiana, J. Hale; Lake Calcashue, near New Orleans [Louisiana], J. G. Anthony) 1 Paratype MCZ 53862 with the label, "Amite River, Mississippi, Mr. Lea drew up his description of the species partly from my specimen." (J. G. Anthony.)

savannahensis Lea, *Unio:* 1857, PANSP, p. 169; 1858, Obs., **6.** p. 81, pl. 16, fig. 61 (Savannah River, also Brantley's Mill, Washington County, Georgia, G. White; Santee Canal, South Carolina, Dr. Ravenel; and Sugar Creek, Mecklenburg County, North Carolina, C. M. Wheatley) 1 Paratype MCZ 178729 ex C. M. Wheatley.

schadei Marshall, *Anodontites:* 1934, Jour. Washington Acad. Sci., **24,** p. 80, figs. 4 6 (Tubicuary River, at Aroja, southern Paraguay, F. Schade) 1 Paratype MCZ 62479 ex F. Schade.

schwerzenbachi 'Parreyss' Bourguignat, *Unio:* 1856, Rev. et Mag. de Zool., (2) **8,** p. 75, pl. 8, figs. 1-5 (Brousse, Anatolie, [Turkey]) 4 Cotypes MCZ 177313 from L. Parreyss ex C. B. Adams coll'n.

scitulus Lea, *Unio:* 1860, PANSP, p. 93; 1860, Obs., **8,** p. 24, pl. 55, fig. 167 (Tuscumbia, Alabama, L. B. Thornton) 1 Idiotype MCZ 178913.

scobinatus Lea, *Unio:* 1856, PANSP, p. 93; 1857, Obs., **6,** p. 19, pl. 26, fig. 13 (Siam, T. R. Ingalls and S. R. House) 3 Paratypes MCZ 175555 ex I. Lea.

scutum Sowerby, *Unio:* 1868, Conchologia Iconica, **16,** pl. 94, fig. 510 (Tenasserim [Burma] Benson, teste Theobold) 1 Paratype MCZ 175548 ex W. Theobold.

secundus Heude, *Pseudodon:* 1877, Conch. Fleuv. Nanking, Part 3, pl. 18, fig. 38 (La rivière Hoai [China] dans la partie moyenne de laquelle il abonde) 2 Paratypes MCZ 167242 ex Musée Heude.

semigranosus Von dem Busch, *Unio:* 1845 [*in* Philippi] Abbild. und Beschr. Conch., **1,** p. 19, pl. 1, figs. 1-3 (Flumen prope Tampico, Mexico) 2 Paratypes MCZ 152861 ex G. Von dem Busch.

semirasa Pilsbry, *Lampsilis:* 1909 [1910], PANSP, p. 534, pl. 26, figs. 7, 8, 9 (Ganina River, 3 miles southwest of San Diequito . . . also in Valles River, two miles above Mecos [Mexico], A. A. Hinkley) 20 Cotypes MCZ 189370 labeled, "Mexico," from A. A. Hinkley ex B. Walker coll'n.

shepardianus Lea, *Unio*: 1834, Tr. APS, **5,** p. 95, pl. 13, fig. 38; 1834, Obs., **1,** pl. 13, fig. 38 (Hopeton, near Darien, Georgia, Prof. Shepard) 3 Paratypes MCZ 155568 ex Prof. Shepard.

showalterii Lea, *Anodonta:* 1860, PANSP, p. 307; 1863, Obs., **9,** p. 37, pl. 33, fig. 284 (Coosa River, Wetumpka, Alabama, E. R. Showalter) 1 Paratype MCZ 178772 ex E. R. Showalter.

showalterii Lea, *Unio:* 1860, PANSP, p. 307; 1862, Obs., **8,** p. 77, pl. 8, fig. 223 (Coosa River, Wetumpka, Alabama, E. R. Showalter) 3 Paratypes MCZ 178920 mentioned by Lea as being in the J. G. Anthony coll'n. 1 Paratype MCZ 178818 ex E. R. Showalter.

shurtleffianus Lea, *Unio:* 1856, PANSP, p. 94; 1857, Obs., **6,** p. 22, pl. 27, fig. 17 (Sina River, India, Major Le Conte; Ahmednugger, India, S. Shurtleff) 1 Paratype MCZ 175566 ex S. Shurtleff.

signata Pilsbry, *Lampsilis:* 1909, PANSP, p. 536, pl. 25, figs. 5, 6; pl. 26, figs. 5, 6 (Valles River, near a small falls about 3 miles below Valles, Mexico, A. A. Hinkley) 10 Cotypes MCZ 192367 ex A. A. Hinkley.

simillimus Ortmann, *Diplodon:* 1921, Mem. Carnegie Mus. [Pittsburgh, Pa.], **8**, p. 495, pl. 35, figs. 3-6; [gills] pl. 45, fig. 2; [glochidia] text fig. 4c (p. 469) (Rio Nhundiaquara, Morretes, Paraná, Brazil, J. D. Haseman) 2 Cotypes MCZ 47050 ex Carnegie Museum.

simplex Lea, *Unio:* 1845, Pr. APS, **10**, p. 163; 1848, Obs., **4**, p. 50, pl. 5, fig. 15 (Black Warrior River, Alabama, B. W. Budd) 1 Idiotype MCZ 178834.

simus Lea, *Unio:* 1838, Tr. APS, **6**, p. 26, pl. 8, fig. 20; 1838, Obs., **2**, p. 26, pl. 8, fig. 20 (Cumberland River, Tennessee, Prof. Troost) 5 Idiotypes MCZ 178903.

sinaloensis Crosse and Fischer, *Anodonta glauca:* 1883, Jour. de Conch., **31**, p. 219 (Rio Presidio in provincia Sinoloa dicta, Reipublicae Mexicanae, A. Forrer) 1 Cotype MCZ 87549 from A. Forrer, ex Boston Soc. Nat. Hist.

sinuosa Morrison, *Guianadesma:* 1943, Nautilus, **57**, p. 46, pl. 8 (Cuyuni River, opposite Kartabo Point, near its junction with the Mazaruni River, Essequibo District, British Guiana) 1 Paratype MCZ 144796 ex U. S. Nat. Mus.

somersii 'Moores' Call, *Anodonta:* 1880, American Naturalist, **14**, p. 530 [Monday Creek, Carbon Hill, Hocking County, Ohio] 3 Cotypes MCZ 158090 [*nomen nudum*] ex R. E. Call coll'n.

sowerbianus Lea, *Unio:* 1833, Tr. APS, **4**, p. 68, pl. 10, fig. 28; 1834, Obs., **1**, p. 180, pl. 10, fig. 28 (Tennessee, G. B. Sowerby) 4 Idiotypes MCZ 178886 from Caney Fork River, Tennessee.

spadiceus Lea, *Unio:* 1857, PANSP, p. 86; 1862, Obs., **8**, p. 59, pl. 1, fig. 201 (Deep River, Gulf, North Carolina, Prof. Emmons; and mountain streams, North Carolina, J. Clark) 3 Idiotypes MCZ 178714.

spatulatus Lea, *Unio:* 1845, Pr. APS, **4**, p. 164; 1848, Obs., **4**, p. 54, pl. 8, fig. 22 (Rock River, Wisconsin, Capt. Maryatt and B. W. Budd) 5 Idiotypes MCZ 178835 from Michigan.

spillmanii Lea, *Margaritana:* 1858, PANSP, p. 138; 1862, Obs., **8**, p. 109, pl. 17, fig. 252 (Tombigbee River, near Columbus, Mississippi, W. Spillman) 1 Paratype MCZ 6395 from Spillman ex R. E. Call coll'n.

spinosus Lea, *Unio:* 1836, Desc. of New Sp. Unio [colored figs.]; 1838, Obs., **2,** p. 57, pl. 16, fig. 50 (Altamaha [River] Hopeton, near Darien, Georgia, J. H. Couper; Altamaha [River] Liberty County, Georgia, L. Le Conte) 5 Paratypes MCZ 87951 from J. H. Couper ex Boston Soc. Nat. Hist.

spinosus Simpson, *Shistodesmus:* see under *vestitus* var. b Heude, *Unio.*

spissus Lea, *Unio:* 1859, PANSP, p. 112; 1859, Obs., **7,** p. 26, pl. 25, fig. 89 (Satilla River, Wayne County, Georgia, T. C. Downie) 4 Metatypes MCZ 178707.

splendidus Lea, *Lampsilis:* 1838, Tr. APS, **6,** p. 70, pl. 19, fig. 61; 1838, Obs., **2,** p. 70, pl. 19, fig. 61 (Altamaha River, near Darien, Georgia, J. H. Cowper [*sic*]) 4 Paratypes MCZ 165692 from J. H. Couper, ex Boston Soc. Nat. Hist.

squameus Lea, *Unio:* 1861, PANSP, p. 391; 1863, Obs., **9,** p. 22, pl. 28, fig. 269 (North Carolina, J. G. Anthony) 1 Paratype MCZ 124889 ex J. G. Anthony.

stagnalis Conrad, *Unio:* 1849, PANSP, p. 152; 1850, JANSP, **1,** p. 275, pl. 37, fig. 2 (Inhabits mill ponds; Ogeechee River, Georgia, J. H. Couper) Holotype MCZ 178778 ex J. H. Couper.

stanleyvillensis Pilsbry and Bequaert, *Caelatura:* 1927, Bull. Amer. Mus. Nat. Hist., **53,** p. 403, pl. 32, figs. 3, 3a, 4; pl. 33, fig. 3. (Congo River at Stanleyville [Belgian Congo], Lang, Chapin, and J. Bequaert) 1 Paratype MCZ 142354. "Is a synonym of *Caelatura* (*Zairia*) *elegans* de Rochebrune." (Bequaert.)

stapes Lea, *Unio:* 1831, Tr. APS, **4,** p. 77, pl. 7, fig. 8; 1834, Obs., **1,** p. 87, pl. 7, fig. 8 (Alabama River [Alabama], Judge Tait) 2 Idiotypes MCZ 178789.

stewardsonii Lea, *Unio:* 1852, Tr. APS, **10,** p. 278, pl. 23, fig. 36; 1852, Obs., **5,** p. 34, pl. 23, fig. 36 (Chattanooga [*sic*] River, Tennessee, T. Stewardson) 6 Idiotypes MCZ 178877.

straitissimus Anthony, *Unio:* 1865, Amer. Jour. Conch., **1,** p. 155, pl. 12, fig. 1 ([Clinch River] Tennessee) Holotype MCZ 17356.

striatus Lea, *Unio:* 1840, Pr. APS, **1,** p. 287; 1842, Obs., **3,** p. 41, pl. 12, fig. 16 (Chattahoochee River, Columbus, Georgia, Dr. Boykin) 4 Idiotypes MCZ 178800.

strodeanus B. H. Wright, *Unio:* 1898, Nautilus, **12,** p. 5 (Escambia River, W. Florida) 6 Paratypes MCZ 210277 from B. H. Wright ex B. Walker coll'n.

strumosus Lea, *Unio:* 1872, PANSP, p. 158; 1874, Obs., **13,** p. 61, pl. 19, fig. 55 (Yadkin River, North Carolina, C. M. Wheatley) 1 Paratype MCZ 30403 ex C. M. Wheatley.

subangulata Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1,** p. 158, pl. 13, fig. 1 ([Shears Lake, Kent County] Michigan) Holotype MCZ 150645.

suberassa Lea, *Anodonta:* 1850 [1851], Pr. Zool. Soc. London, p. 198; 1860, Obs., **7,** p. 54, pl. 33, fig. 115 (Laguna de Bai, Luzon, Philippines, H. Cuming) 2 Paratypes MCZ 175579 ex H. Cuming.

suberoceus Conrad, *Unio:* 1854, JANSP, **2,** p. 297, pl. 27, fig. 1 (One of the tributaries to Canadian River, Arkansas, Dr. Woodhouse) 1 Idiotype MCZ 178693.

subellipsis Lea, *Unio:* 1856, PANSP, p. 262; 1858, Obs., **6,** p. 62, pl. 10, fig. 44 (Creeks near Columbus, Georgia, Bishop Elliott) 2 Idiotypes MCZ 178934.

subflavus Lea, *Unio:* 1857, PANSP, p. 170; 1858, Obs., **6,** p. 90, pl. 19, fig. 70 (Walnut Creek, above Macon, Georgia, Bishop Elliott and J. C. Plant) 2 Idiotypes MCZ 72523.

subgibbosa Anthony, *Anodon:* 1866, Amer. Jour. Conch., **2,** p. 144, pl. 6, fig. 2 (Black Lake, Michigan) Holotype MCZ 161854.

sub-inflata Anthony, *Anodon:* 1865, Amer. Jour. Conch., **1,** p. 160, pl. 15, fig. 1 (Michigan) Holotype MCZ 161863.

sublatus Lea, *Unio:* 1857, PANSP, p. 169; 1858, Obs., **6,** p. 82, pl. 16, fig. 62 (Uchee Bar, below Columbus, Georgia, Bishop Elliott) 2 Idiotypes MCZ 124882.

succineus Heude, *Mycetopus:* 1885, Conch. Fleuv. Nanking, Part 9, pl. 70, fig. 134 (Les rivières de Lu-tcheou fou et de Tong-teh'eng vers leur embouchure dans le lac Teh'ao, province de Ngan-houé [China]) 1 Paratype MCZ 167109 ex Musée Heude.

sumatrensis Lea, *Unio:* 1859, PANSP, p. 153; 1860, Obs., **7,** p. 57, pl. 34, fig. 118 (Sumatra, H. Cuming) 2 Paratypes MCZ 175563 ex H. Cuming. The name was changed to *dimotus* by Lea 1870, because *sumatrensis* was preoccupied for a *Unio* by Dunker.

superbus Lea, *Unio:* 1843, Desc. 12 Uniones [no pagination]; 1848, Obs., **4,** p. 39, pl. 42, fig. 11 (New Holland [Australia], J. C. Jay) 2 Idiotypes MCZ 175551 from Siam.

superiorensis Marsh, *Unio:* 1897, Nautilus, **10,** p. 103, pl. 1, figs. 1, 2, 5 (Michipicoton River, upper shore of Lake Superior, Canada, J. H. Ferris) 1 Cotype MCZ 20169 from J. H. Ferris ex L. S. Frierson.

suttoni B. H. Wright, *Unio:* 1897, Nautilus, **11.** p. 56 (Lake near Candler, Marion County, Florida, B. Sutton) 2 Paratypes MCZ 20172 from B. H. Wright ex L. S. Frierson.

symmetricus Lea, *Unio:* 1845, Pr. APS, **4.** p. 164; 1848, Obs., **4.** p. 47, pl. 4, fig. 11 (Red River, at Alexandria, Louisiana, J. Hale) 2 Idiotypes MCZ 178732.

taitianus Lea, *Unio:* 1834, Tr. APS, **5.** p. 39, pl. 4, fig. 11; 1834, Obs., **1.** p. 151, pl. 4, fig. 11 (Alabama River [Alabama], Judge Tait) 1 Idiotype MCZ 178811.

tennesseensis Frierson, *Strophitus undulatus:* 1927, Check list N. American Naiades, Waco, Texas, p. 22 (Headwaters of the Tennessee River). Lectotype, here selected, MCZ 16690, Pl. 2, fig. 1. The original description is here repeated, "A form found in the headwaters of the Tennessee River, very thin, much compressed, widely biangulated behind, yellow inside and out," ex L. S. Frierson.

tenuis Lea, *Anodonta:* 1850 [1851] Pr. Zool. Soc. London, p. 198; 1860, Obs., **7.** p. 55, pl. 33, fig. 116 (Sual, Luzon, Philippines, H. Cuming) 4 Paratypes MCZ 175578 ex H. Cuming.

tenuiseulus Frierson, *Unio:* 1911, Nautilus, **25.** p. 29, pl. 1, figs. 4-6 (Reedy Lake, Polk County, Florida) 3 Cotypes MCZ 20180 ex L. S. Frierson.

tetricus Lea, *Unio:* 1857, PANSP, p. 170; 1859, Obs., **7.** p. 13, pl. 22, fig. 78 (Flint River, near Albany, Georgia, Bishop Elliott) 2 Idiotypes MCZ 178722.

texasensis Lea, *Unio:* 1860, JANSP, **4.** p. 359, pl. 61, fig. 184; 1860, Obs., **8.** p. 41, pl. 61, fig. 184 (Dewitt County, Texas, W. Newcomb) 4 Paratypes MCZ 178921 ex W. Newcomb.

thaanumi Schlesch, *Anodonta piscinalis:* 1907, Ann. Soc. Roy. Mal. Belgique, (2) **42.** p. 161 (in Zwei Teichenhinter "Gl. Carlsberg" in valby bei Kopenhagen [Denmark]) 9 Cotypes MCZ 192022 ex D. Thaanum coll'n.

thorntonii Lea, *Unio:* 1857, PANSP, p. 83; 1867, Obs., **11.** p. 42, pl. 14, fig. 36 (Tuscumbia, Alabama, L. B. Thornton) 8 Paratypes MCZ 178809 ex L. B. Thornton.

tinkeri B. H. Wright, *Unio:* 1899, Nautilus, **13.** p. 7 (Tombigbee River [Moscow] Alabama) 2 Paratypes MCZ 20165 ex L. S. Frierson.

tombigbeanum Frierson, *Pleurobema:* 1908, Nautilus, **22.** p. 27, pl. 3, figs. 3, 4 (Tombigbee River, Demopolis, Marengo County, Alabama; Columbus, Mississippi) 2 Idiotypes MCZ 178824 from the Alabama River, Selma, Alabama.

tombigbeensis Lea, *Margaritana:* 1858, PANSP, p. 138; 1862, Obs., **8**, p. 111, pl. 18, fig. 255 (Tombigbee River, near Columbus, Mississippi, W. Spillman) 1 Paratype MCZ 152037 ex W. Spillman.

tortivus Lea, *Unio:* 1840, Pr. APS, **1**, p. 287; 1842, Obs., **3**, p. 42, pl. 12, fig. 17 (Chattahoochee River, Columbus, Georgia, Dr. Boykin) 3 Idiotypes MCZ 178688.

triangulata Lea, *Margaritana:* 1858, PANSP, p. 138; 1859, Obs., **7**, p. 46, pl. 32, fig. 111 (Upper Chattahoochee, Georgia, Bishop Elliott; Columbus, Georgia, Dr. Boykin and J. Postell; Polato County, Georgia, G. White; Sawney's Creek, South Carolina, Dr. Blanding) 3 Paratypes MCZ 165696 from Columbus, Georgia, from the E. R. Mayo coll'n ex Boston Soc. Nat. Hist.; 2 Idiotypes MCZ 150661.

triclarus Heude, *Unio:* 1877, Conch. Fleuv. Nanking, Part 2, pl. 10, figs. 21, 21a (La rivière Siang (prov. de Hou-Nan) [China]) 1 Paratype MCZ 167111 ex Musée Heude.

triembolus Benson, *Unio:* 1862, Ann. Mag. Nat. Hist., (3) **10**, p. 190, (flumina Ramgunga, prope Moradabad [India]) 3 Cotypes MCZ 175558 ex W. H. Benson.

triumphans B. H. Wright, *Unio:* 1898, Nautilus, **11**, p. 101 (Coosa River, St. Clair County, Alabama) 2 Paratypes MCZ 139625 ex B. Walker coll'n.

trochelianus Lea, *Unio:* 1852, Tr. APS, **10**, p. 280, pl. 23, fig. 39; 1852, Obs., **5**, p. 36, pl. 23, fig. 39 (Coosawatte River, Murray County, Georgia, Dr. Boykin) 1 Idiotype MCZ 178810.

trompi Drouet and Chaper, *Unio:* 1892, Mém. Soc. Zool. France, **5**, p. 153, pl. 6, figs. 8-10 (le Kapoeas (Semitau) à Borneo) 1 Cotype MCZ 174098 ex S. Putzeys coll'n.

troostensis Lea, *Unio:* 1834, Tr. APS, **5**, p. 71, pl. 10, fig. 30; 1834, Obs., **1**, p. 183, pl. 10, fig. 30 (Cumberland River [Tennessee], Prof. Troost) 3 Idiotypes MCZ 178922.

truncata B. H. Wright, *Margaritana marginata:* 1898, Nautilus, **11**, p. 124 (It occurs in eastern as well as western waters and into Virginia and Tennessee) 4 Cotypes MCZ 152253 from Greyson County, Virginia ex B. H. Wright.

tuberosus Lea, *Unio:* 1840, Pr. APS, **1**, p. 286; 1842, Obs., **3**, p. 48, pl. 14, fig. 25 (Cany Fork and Cumberland Rivers, Middle Tennessee, S. M. Edgar) 2½ Paratypes MCZ 6205 from the Cumberland River, mentioned by Lea as being in the Troost coll'n., ex R. E. Call coll'n.

tumidus Morelet, *Monocondylus:* 1866, Jour. de Conch., **14,** p. 62 (In torrentibus montanis Cambodiae); 1875, Series Conchologique Part 4, p. 337, pl. 16, fig. 1; type figured, Jour. de Conch., **90,** pl. 3, figs. 42-44. 3 Paratypes MCZ 175576 ex A. Morelet.

tuomeyi Lea, *Unio:* 1852, Tr. APS, **10,** p. 256, pl. 13, fig. 4; 1852, Obs., **5,** p. 12, pl. 13, fig. 4 (Abbeville District, South Carolina, J. P. Barratt) 1 Idiotype MCZ 178699.

turcicus 'Parreiss' [*sic*] Kuster, *Unio:* 1862, Conch. Cabinet, (2) **9,** Part 2, p. 267, pl. 90, figs. 3-4 (Kleinasien [Turkey]) 2 Cotypes MCZ 152877 from L. Parreyss ex C. B. Adams coll'n.

turgidulus Lea, *Unio:* 1858, PANSP, p. 40; 1862, Obs., **8,** p. 66, pl. 5, fig. 211 (Cumberland River, Prof. Troost and T. C. Downie; Florence, Alabama, G. White) 3 Idiotypes MCZ 178565.

turgidus Lea, *Unio:* 1838, Tr. APS, **6,** p. 11, pl. 5, fig. 11; 1838, Obs., **2,** p. 11, pl. 5, fig. 11 (near New Orleans [Louisiana], Mr. Barabino) 2 Idiotypes MCZ 178832.

umbrans Lea, *Unio:* 1857, PANSP, p. 104; 1858, Obs., **6,** p. 72, pl. 13, fig. 53 (Othcalooga Creek, Gordon County, Georgia, Bishop Elliott) 2 Idiotypes MCZ 178874.

umbrosa Lea, *Unio:* 1856, PANSP, p. 95; 1857, Obs., **6,** p. 31, pl. 30, fig. 26 (Mendellin River [near Vera Cruz] Mexico, Dr. Burrough) 1 Paratype MCZ 178872 from Dr. Burrough, mentioned by Lea as being in the J. G. Anthony coll'n.

undivaga Pilsbry, *Unio:* 1909, PANSP, p. 536, pl. 26, figs. 1-4; pl. 27, fig. 5 (Valles River, two miles above Mecos in a muddy bank just above the rapids, A. A. Hinkley) 3 Cotypes MCZ 30633 from A. A. Hinkley ex B. Walker coll'n.

unicolor Lea, *Unio:* 1845, Tr. APS, **4,** p. 163; 1848, Obs., **4,** p. 48, pl. 4, fig. 12 (Tuscaloosa, Alabama, W. B. Budd) 6 Idiotypes MCZ 178909 from the Pearl River, Alabama.

unicostatus B. H. Wright, *Unio:* 1899, Nautilus, **13,** p. 69 (Spring Creek, Decatur County Georgia) 2 Paratypes MCZ 20150 ex L. S. Frierson.

upsoni Marsh, *Unio:* 1880 "Read before the Mercer County, Illinois Scientific and Historical Society March 2, 1880. Mr. Marsh had copies of the description published and thinks that the species was described on the records. It was not figured," Simpson, 1900, Pr. U. S. Nat. Mus., **22,** p. 539; Marsh, 1887 Conch. Exch., **1,** p. 51 (Kishaeaukee River, Winnebago County, Illinois) 1 Cotype MCZ 5551 from W. A. Marsh ex R. E. Call coll'n.

vanuxemensis Lea, *Unio:* 1838, Tr. APS, **6,** p. 36, pl. 11, fig. 31; 1838, Obs., **2,** p. 36, pl. 11, fig. 31 (Cumberland River, Tennessee, Prof. Troost) 1 Idiotype MCZ 178888.

venustus Lea, *Unio:* 1838, Tr. APS, **6,** p. 4, pl. 2, fig. 4; 1838, Obs., **2,** p. 4, pl. 4, fig. 4 (Potosi, Missouri, John Perry; Cincinnati, Ohio, T. G. Lea) 5 Idiotypes MCZ 178880.

verus Lea, *Unio:* 1860, PANSP, p. 140; 1862, Obs., **8,** p. 87, pl. 11, fig. 231 (Cahawba River, Perry County, Alabama, E. R. Showalter) 1 Paratype MCZ 178798 mentioned by Lea as being in the J. G. Anthony coll'n.

vestitus var. *a* Heude, *Unio:* 1883, Conch. Fleuv. Nanking, Part 8, pl. 58, fig. 112 (La rivière de Ning-kouo fou, celle de T'sing-yang hien (Ngan-houé) [China]) 1½ Paratypes MCZ 167241 ex Musée Heude. This name was preoccupied by Lea for a *Unio,* therefore Simpson, 1900 Pr. U. S. Nat. Mus., **22,** p. 801 changed it to *Quadrula ovata.*

vestitus var. *b* Heude, *Unio:* 1883, Conch. Fleuv. Nanking, Part 8, pl. 59, fig. 115 (La rivière de Ning-kouo fou, celle de T'sing-yang hien (Ngan-houé) [China]) 1½ Paratypes MCZ 167245 ex Musée Heude. This name was preoccupied by Lea for a *Unio,* therefore Simpson, 1900, Pr. U. S. Nat. Mus., **22,** p. 804 changed it to *Shistodesmus spinosus.*

villosa B. H. Wright, *Unio:* 1898, Nautilus, **12,** p. 32 (Suwannee River, Suwannee Co., Florida) 1 Paratype MCZ 186836 ex B. H. Wright.

virescens Lea, *Unio:* 1858, PANSP, p. 40; 1860, Obs., **8,** p. 23, pl. 55, fig. 166 (Tennessee River at Tuscumbia, Alabama, B. Pybas) 6 Paratypes MCZ 178829 ex Pybas and Thornton, mentioned by Lea as being in both collections.

vondenbushiana [*sic*] Lea, *Margaritana:* 1840, Pr. APS, **1,** p. 288; 1842, Obs., **3,** p. 60, pl. 18, fig. 39 (Java, G. Von dem Busch) 2 Paratypes MCZ 175596 ex G. Von dem Busch.

walkeri B. H. Wright, *Unio:* 1897, Nautilus, **11,** p. 91; figured by Simpson, 1900, PANSP, p. 77, pl. 1, fig. 5 (Suwannee River, Madison County, Florida) 2 Paratypes MCZ 20178 ex L. S. Frierson.

walpolei Hanley, *Monocondylaea:* 1871, Pr. Zool. Soc. London, p. 587 (Sarawak, Borneo) Lectotype MCZ 175577 selected by Johnson, 1948, Nautilus, **62,** p. 49, pl. 3, fig. 2 ex R. F. Geale.

waltoni B. H. Wright, *Unio:* 1888, PANSP, p. 114, pl. 2, fig. 3 (Lake Woodruff, Volusia County, Florida) 7 Paratypes MCZ 167701 from B. H. Wright ex B. Walker coll'n.

wardiana Lea, *Anodonta:* 1838, Tr. APS, **6,** p. 46, pl. 14, fig. 42; 1838, Obs., **2,** p. 46, pl. 14, fig. 42 (Near Chilicothe, Ohio, J. C. Ward) 1 Paratype MCZ 37229 ex J. C. Ward.

wardii Lea, *Unio:* 1861, PANSP, p. 392; 1863, Obs., **9,** p. 9, pl. 24, fig. 257 (Walhonding River, Ohio, J. C. Ward; Wassepinicon River, Iowa, Dr. Foreman; Coal River, Logan County, Virginia, Dr. Hartmann and Mr. Anthony) 1 Paratype MCZ 178774 from Dr. Hartmann ex J. G. Anthony. "The specimen from Mr. Anthony is marked 'Tennessee,' but Dr. Hartmann, on seeing this specimen, thinks he recognizes it as the specimen which he gave Mr. Anthony from the same habitat (Coal River, Virginia) with his own." (Lea).

watersoni Tomlin, *Anodonta:* 1923, Jour. of Conch., **17,** p. 68, (Lake Beschik, Salonika [Greece]) 2 Paratypes MCZ 78226 ex J. R. Le B. Tomlin.

webbianus B. H. Wright, *Unio* (*Elliptio*): 1934, Nautilus, **47,** p. 94, pl. 10, figs. 1-2 (Lake Consuelo, Citrus County, Florida, near Floral City) 2 Paratypes MCZ 95548 ex B. H. Wright.

websterii B. H. Wright, *Unio:* 1888, PANSP, p. 113, pl. 2, fig. 2 (Lake Woodruff, Volusia County, Florida) 1 Paratype MCZ 178765 ex B. H. Wright.

wheatleyi Lea, *Anodonta:* 1852, Tr. APS, **10,** p. 287, pl. 26, fig. 49; 1852, Obs., **5,** p. 43, pl. 26, fig. 49 (Para [Brazil] South America, C. M. Wheatley) 3 Paratypes MCZ 192020 ex C. M. Wheatley.

wheatleyi Lea, *Monocondylaea:* 1862, PANSP, p. 176; 1863, Obs., **10,** p. 35, pl. 50, fig. 307 (River Tigris, Assyria [Iraq], C. M. Wheatley) 1 Paratype MCZ 178755 ex C. M. Wheatley.

wheatleyi Lea, *Unio:* 1857, PANSP, p. 85; 1860, Obs., **8,** p. 58, pl. 1, fig. 200. [The name was herein changed by Lea to *Unio catawbensis*, *wheatleyi* being preoccupied.] (Catawba River, Gaston County, North Carolina, C. M. Wheatley) 1 Idiotype MCZ 20166 from Ashley's Creek, Mecklenberg County, North Carolina. From C. M. Wheatley ex L. S. Frierson.

wheeleri Ortmann and Walker, *Arkansia:* 1912, Nautilus, **25,** p. 98, pl. 8 (Old River, Arkadelphia, Arkansas, H. E. Wheeler) 1 Paratype MCZ 135712 from H. E. Wheeler ex Boston Soc. Nat. Hist.; 1 Paratype MCZ 23319 from H. E. Wheeler ex L. S. Frierson.

woodwardianus Lea, *Unio:* 1859, JANSP, **4,** p. 199, pl. 23, fig. 82; 1859, Obs., **7,** p. 17, pl. 23, fig. 82; [anatomy] pl. 29, fig. 103 (Etowah and Connasauga Rivers, Cass County, Georgia, Bishop Elliott and G. White) 5 Idiotypes MCZ 192019.

zeiglerianus Lea, *Unio:* 1838, Tr. APS, **6,** p. 32, pl. 10, fig. 27; 1838, Obs., **2,** p. 32, pl. 10, fig. 27 (Cumberland River, Tennessee, Prof. Troost) 2 Idiotypes MCZ 178893.

zonatus Heude, *Unio:* 1883, Conch. Fleuv. Nanking, Part 8, pl. 61, fig. 120 (La rivière de Ning-kouo fou, au sud de la ville [China]) 1 Paratype MCZ 167112 ex Musée Heude.

PLATES

PLATE 1

Fig. 1. *Anodonta bellua* Morelet. Lacu Toui-Sap, Cambodia. Lectotype MCZ 175610. Natural size.

Fig. 2. *Unio bolli* Call. Colorado River [Austin] Texas. Lectotype MCZ 5017. Natural size.

PLATE 1

PLATE 2

Fig. 1. *Strophitus undulatus tennesseensis* Frierson. Headwaters of the Tennessee River. Lectotype MCZ 16690. Natural size.

Fig. 2. *Unio ascia* 'Benson' Hanley. Penang [Straits Settlements]. Lectotype MCZ 17046. Natural size.

Fig. 3. *Unio cor* Conrad. Elk and Flint Rivers, Alabama. Holotype MCZ 178792. Natural size.

Fig. 4. *Quadrula granifera pusilla* Simpson. Green River at Mammoth Cave, Kentucky. Lectotype MCZ 20176. Natural size.

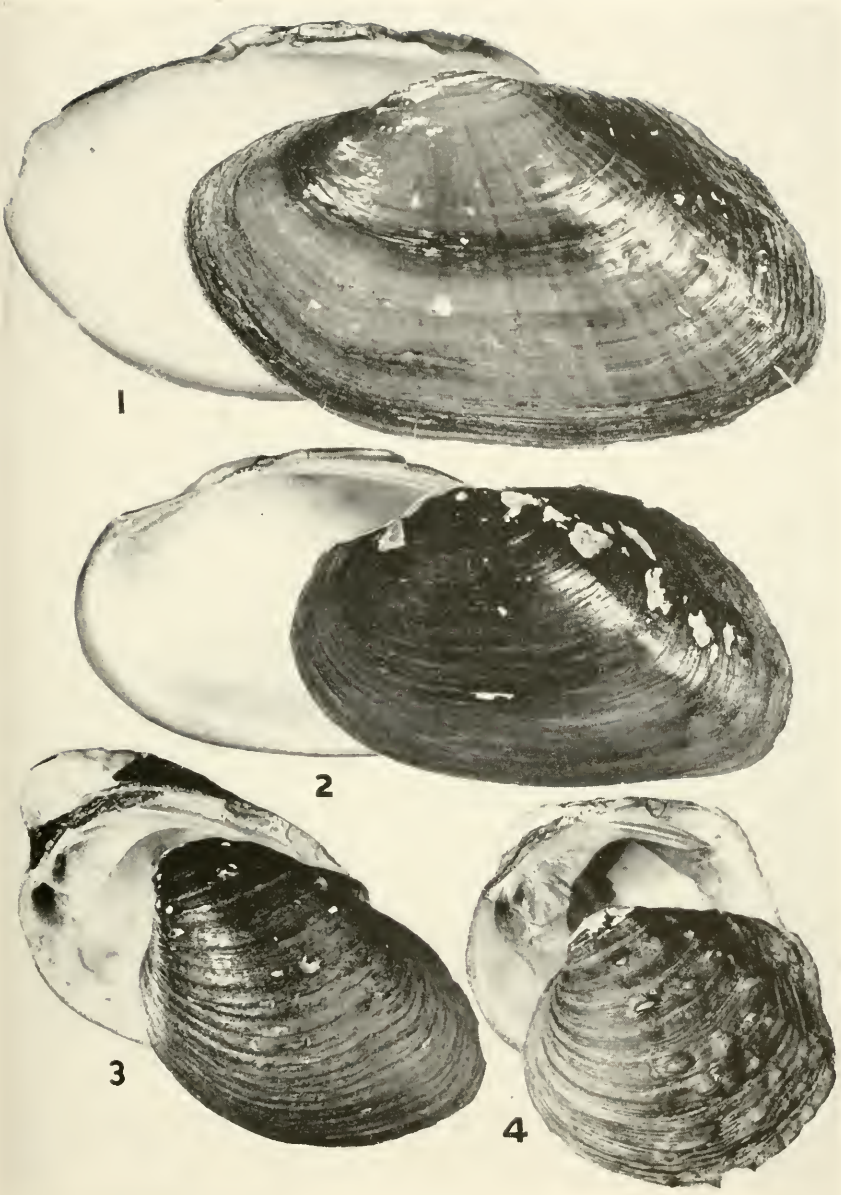


PLATE 2

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 5

PSEUDEMYS SCRIPTA CALLIROSTRIS FROM VENEZUELA WITH A GENERAL SURVEY OF THE *SCRIPTA* SERIES

By Ernest Williams

With Three Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
September, 1956

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY

AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 115.

Breviora (octavo) 1952 — No. 61 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899-1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 115, No. 5

PSEUDEMYS SCRIPTA CALLIROSTRIS FROM VENEZUELA WITH A GENERAL SURVEY OF THE *SCRIPTA* SERIES

By Ernest Williams

With Three Plates

CAMBRIDGE, MASS., U. S. A.

PRINTED FOR THE MUSEUM

September, 1956

No. 5 — Pseudemys scripta callirostris *from Venezuela with a general survey of the* scripta *series*

By Ernest Williams

In 1947 Benjamin Shreve reported a juvenile *Pseudemys* from the Falcon district of Venezuela, assigning it to the *scripta* group but not further identifying it. Re-examination of this specimen has revealed that it is referable to *callirostris* Gray and is the most easterly record to date of this form.

In the course of identifying this individual I have looked into the *scripta* series as a whole and I will therefore present a few comments here on the overall picture. This portion of the discussion is intended to be suggestive rather than definitive. A rather full record in regard to *callirostris* is included since there is no adequate account in English.

TAXONOMIC HISTORY

John Edward Gray in 1855 described *Emys callirostris* — "The Beautiful Beaked Emys" — from a single specimen, stuffed, half-grown, presented by the Haslar Hospital with the locality "America." Gray furnished in his plate XIIb an excellent figure of dorsal and ventral views of the type showing the "symmetrical rings" on the chin which were the most distinctive feature of the form, and the occasion of the specific name.

In his description of the type, Gray recognized the close relationship of this form to "*Emys ornata*" and in 1863 (again in 1870) placed *callirostris* in the genus *Callichelys* of which *ornata* was the type.

Günther (1885) was apparently the first to suggest that *callirostris* may have come from the "West coast of Central America." Cope (1887) followed, listing *Pseudemys callirostris* from Central America. Boulenger (1889) did not suggest any locality for *callirostris* but, though listing it as a variety, thought it was perhaps only an individual variation of *Chrysemys ornata*.

The second specimen of *callirostris* was described by Siebenrock (1907) who regarded it as representative of a distinct subspecies of *Chrysemys ornata* but doubted the ostensible locality — "Florida" — of his specimen since he had received it from a

dealer. He abstracted his 1907 information in his 1909 "Synopsis."

The next notice of *callirostris* was as a full species in the list of Mertens and Müller (*in* Hans Rust, 1934). The reason for this treatment was not revealed until Müller's paper of 1940.

In the interval, however, Carr (1938) (in a paper primarily concerned with indicating intergradation between *Pseudemys scripta elegans*, then called *troosti*, and populations of the northeast coast of Mexico which he called *cataspila*) mentioned *callirostris* rather parenthetically. He wrote: "Gray's description of the form (1855) is based on a single specimen and the characters by which he distinguishes it all fall within the range of individual variation in *cataspila*. I am inclined to agree with Boulenger that Gray's specimen was an aberrant *cataspila*." Carr was apparently unaware of Siebenrock's second specimen, although he cites the 1909 Synopsis.

In 1940, in a paper which (because of World War II and because of its rather obscure place of publication) has not been generally available to American herpetologists, Lorenz Müller redescribed *callirostris* from a series of 10 specimens in the Münchener Zoologische Staatssammlung.

Of Müller's seven specimens with good locality data, three came from Barranquilla, Colombia, and four were collected by Hellmich at Jesus del Rio in a tributary of the Rio Magdalena. Müller published excellent photographs of the young and half grown and full descriptions of these and of an adult, comparing them pictorially and in the text with comparable stages of *ornata*.

In 1950 Smith and Taylor cited *callirostris* in their checklist as a possible synonym of *Pseudemys scripta cataspila* (and injudiciously restricted the type locality to Alvarado, Vera Cruz, Mexico).

In 1952 Mertens published a discussion, with photographs, of two more living specimens from the vicinity of Barranquilla. He mentioned also another probable record of the form (Stuve, 1907 [1]) from the neighborhood of Soplaviento on the lower Magdalena.

1 Wochenschr. Aquar. Terr. 4, 228-229 (not seen).

Mertens and Wermuth (1955) list *Pseudemys callirostris* as a full species with the distribution "Northern South America (Colombia)."

CHARACTERS

The distinctive characters of *callirostris* as compared with *ornata* have been stated by Gray (1855), Siebenrock (1909), and Mertens (1952). Lorenz Müller's discussion, though more lengthy and based on more material than any other, does not state what characters are diagnostic but merely alternates detailed descriptions of individual specimens of *callirostris* and *ornata*. I summarize in Table 1 the characters found to be valuable.

TABLE 1

callirostris	*ornata*
1. a broad supratemporal stripe or spot cinnabar red in life, usually rounded off anteriorly and well separated from the orbit.	1. a narrow supratemporal stripe, yellowish or reddish in life, typically entering the orbit.
2. a variable number of *ocelli* on the underside of the snout and on the maxillary area. Ocelli (usually 3) on the mandible. Less regular ocelli posteriorly on the throat.	2. rather narrow *stripes* on the underside of the snout, the maxillary area and the mandible. The mandible typically with three very elongate spots which may either round off posteriorly or may connect in variable fashion with one or more of the stripes on the throat.

Siebenrock could find no characters of the shell to distinguish *callirostris* from *ornata*, nor can I. Various statements made by Müller implying shell differences require confirmation. He suggests, for example, that in the adult state the dorsal ocellar pattern is less clearly shown in *callirostris* than in *ornata* and that the shell is thus more "eintönig." He finds differences also in shell shape, plastral proportions, etc.

The ocellar as opposed to striped pattern of chin and snout appears to be a quite constant difference between all known *callirostris* (15+) and every *ornata* seen by me [1] or figured in

[1] All specimens of *ornata* in the collections of the American Museum of Natural History, the Chicago Natural History Museum, the Philadelphia Academy of Natural Sciences and the United States National Museum have been examined as well as all *ornata* in the Museum of Comparative Zoology.

the literature. Indeed, in this respect *callirostris* differs from all other members of the *scripta* series. (There is some approach in this character however in *P. s. gaigeae* Hartweg in which the lateral stripes are shortened to long ovals.)

The supratemporal spot seems not to be constant to the same degree. Müller mentions that in one of his specimens of *callirostris* this spot was well separated from the orbit on one side, but narrowed forward and approached the orbit very closely on the other. Further, a series of specimens from Costa Rica (Coen Dispensary, MCZ 19351-3) show supratemporal spots not entering the eye, much as in *callirostris*. This is surprising since all the Panamanian specimens which I have seen (and an Antioquia, Colombia specimen) have supratemporal stripes entering the eye quite as in Honduran or Mexican *ornata*.

There appears to be, however, much parallelism within *scripta* in regard to the development of a supratemporal spot. Thus *Pseudemys scripta gaigeae* is essentially only a regional variety in which just such a supratemporal spot as is found in *callirostris* or the Costa Rica individuals is especially well defined. *Pseudemys scripta elegans* also approaches *callirostris* in this regard though in that form the supratemporal spot regularly enters the orbit. In each of these cases also the supratemporal spot is red whereas the similarly placed stripe of neighboring forms is yellow.

As compared with all previously illustrated Colombian *callirostris* the Venezuelan specimen (Plate 2) appears to differ by the narrowness of the central figure on the plastron. Probably, however, there is high individual variability in this character. There is certainly extreme variability in this regard within *ornata* and except, perhaps, in very local populations there appears to be no geographical pattern to the variation.

DISTRIBUTION

Callirostris has previously been reported from only three localities in Colombia: (1) the vicinity of Barranquilla; (2) Jesus del Rio (Departamento Bolivar) between Calamar and Magangue; (3) near Soplaviento. In addition, Brother Niceforo Maria informs me that two additional localities are represented in the collections of the Instituto de la Salle: the Canal del Dique

(Bolivar), not far from Barranquilla, and the borders of the Cienaga del Guajaro (Atlantico), again near Barranquilla. The United States National Museum also has a specimen from Cartagena (USNM 61676).[1]

The new record in the Falcon district of Venezuela at La Penita and Maravita Springs, Cerro Chichiriviche extends the known range of *callirostris* hundreds of miles to the east. That an extension of this magnitude is possible, points, as does the general inadequacy of our knowledge of *callirostris,* to the extreme imperfection of our information regarding the turtles of South America.

There is no ground for assuming that the eastern boundary of *callirostris* has been discovered. Between the Venezuelan record and *Pseudemys dorbigni* of South Brasil and Argentina there is an immense gap which, though it may be in great part real, will bear investigation.

As regards the western boundary of *callirostris* there is no exact knowledge either. From the Rio Chepo on the west coast of Panama the Museum of Comparative Zoology has a typical specimen of *ornata* (MCZ 7868). The American Museum has a number of *ornata* from various localities in the Canal Zone. They are again essentially typical. The Chicago Natural History Museum has the most easterly specimen (CNHM 63902) referable to *ornata* known to me — from Turbo, Gulf of Uraba, Antioquia, Colombia. This individual has a *broad* supratemporal stripe entering the eye and an extraordinarily reduced plastral pattern. This single individual is not typical of, but neither is it outside the variability of, *ornata.* The broad supratemporal stripe probably betrays some influence of *callirostris,* but only further knowledge of the Uraba Turbo population can show whether there is true intergradation.

AFFINITIES

Certainly, in most characters *callirostris* is extremely close to *ornata.* It is closer to this than to any other form. From this point of view Siebenrock was justified in regarding it as a subspecies of *ornata.* However, it seems advisable to view this form

1 Dr. F. Medem is making more extensive collections of *callirostris* in Colombia upon which he will report.

in a larger context, in terms of the entire series related to *P. scripta* to which it certainly belongs.

I have not attempted to review the *scripta* series in a thorough fashion; to do so will require many more specimens from many more localities than have been available to me. But in order to make clear the place of *callirostris* in the *scripta* series I have examined juveniles of every member of this widely distributed series, except *nebulosa* and *hiltoni*, and adults of most forms including both *nebulosa* and *hiltoni*.

In this series the most striking differences are those in pattern, and these are most clearly seen in juveniles. Fully adult animals of either sex may show patterns much more obscurely, and in adult males the phenomenon which is commonly called "melanism" typically results in the complete disruption of the juvenile pattern.

I state the geographic variation in pattern in terms of four conspicuous elements only — the dorsal carapace pattern, the pattern of the sides of the head, of the chin, and of the plastron.

1. The *scripta* series begins on the east coast of North America with the populations called *scripta*. These populations extending from southeastern Virginia to northern Florida have a carapace typically with a transverse stripe on each costal though occasionally the last costals may bear ocelli, a head pattern with a very conspicuous *vertical yellow* spot behind the eye (the spot usually shaped like a distorted triangle), a chin which is striped longitudinally, and a plastral pattern varying from immaculate yellow to ocelli or smudges on each plastral scute.

2. To the west the *scripta* populations intergrade with populations given the name of *elegans*, occupying the Mississippi Valley from Illinois to the Gulf, ranging westward into Iowa, Kansas, Missouri, Oklahoma and Texas, eastward into Alabama, Tennessee, Kentucky and Ohio. These populations centering on the Mississippi Valley resemble *scripta* in the transversely lined carapace. They differ strikingly in the presence of a *longitudinal red* temporal spot behind the eye. The chin is longitudinally striped, while the plastral pattern is typically one of open ocelli in juveniles or smudges in adults, one on each plastral scute.

3. In the upper courses of the Cumberland and Tennessee rivers, populations formerly regarded as not distinct from *elegans* have recently been redescribed under the name *troosti*.

These animals have transverse carapace striping,[1] a *narrow longitudinal yellow* head spot, chin with broad stripes, and on the plastron small ocelli or smudges or no dark pigmentation.

4. In portions of Chihuahua, Coahuila, Durango and extreme western Texas, there is a population (*P. s. gaigeae*) which in typical specimens is very distinctive but which apparently intergrades broadly and complexly to the east with *elegans* and to the south with the form sometimes called *cataspila* but which I would unite with *ornata*. *Gaigeae* has a reticulate carapace pattern with frequently some ocelli present at least posteriorly, a *black-bordered oval red* spot behind the eye and well separated from it, a chin striped medially but with the lateral stripes shortened into elongate ovals that are almost ocelli, and a plastral pattern of broken lines and spots mostly extending laterally

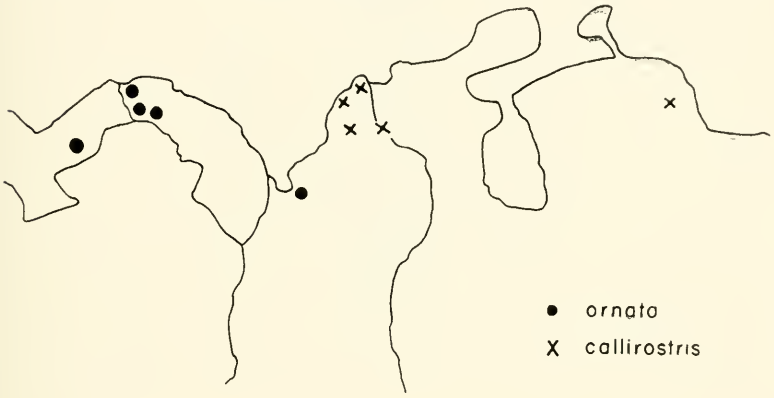


Fig. 1. Map of the southernmost localities (Panama and Colombia) for *Pseudemys scripta ornata* and the known localities for *Pseudemys scripta callirostris* (Colombia and Venezuela).

along the sulci. The plastral pattern may sometimes approach that of *scripta* and sometimes be more like that of *ornata* (see below) but is never as well defined as in either of these.

1 MCZ 4905, a juvenile from Knoxville, Tennessee, regarded as *troosti* on balance of characters and on locality, is highly peculiar in several aspects of dorsal pattern especially in having a rather ocellar light spot in *each* costal rather than the transverse stripe. This specimen is figured in ventral view in Plate 1.

5. To the west of *gaigeae* in Mexico there is another population in southern Sonora which has been described under the name of *hiltoni*. The carapace is reticulate dorsally. There is a longitudinal light orange temporal spot behind the eye, not black-bordered and not separated from the eye. The chin is striped, and the plastral pattern is one of discrete paired, rather rectangular, smudges arranged in two lines along the middle of the plastron (Fig. 1). This population is not known to intergrade with *gaigeae* or *ornata*, but *Pseudemys* from intermediate localities are still undiscovered.

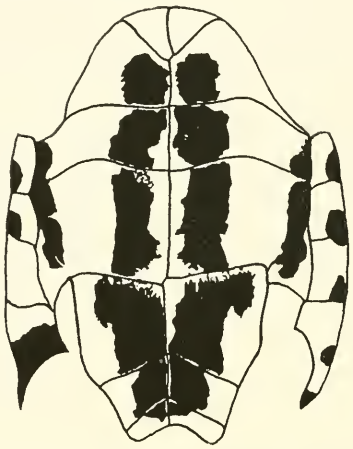


Fig. 2. Plastral pattern in *Pseudemys scripta hiltoni* type. (After Carr 1942.)

6. Across the Gulf of Baja California in the southern part of the peninsula of that name is an isolated population named *nebulosa* by Van Denburgh (1895). This form is described as having rather reticulate markings dorsally on the carapace, an orange or yellow spot, not black-bordered, on the side of the head, a striped chin, and (Fig. 2) a narrow smudged central plastral pattern, not broken into discrete spots, much resembling the plastral figure of *Chrysemys picta marginata* and with obvious similarities also to the plastral pattern of *ornata* (see below). A specimen (USNM 75354) from La Purisima, La Paz, Lower California has a plastral figure of broken smudges very

like those of the type series of *hiltoni*, which may thus be synonymous with *nebulosa* — the earlier named of the two forms.

7. I distinguish in the remaining portions of Mexico and in all of Central America only a single member of the *scripta* series (I omit *P. grayi* from discussion for the moment). This set of populations is variable but not in any defined geographical sense; there is certainly no *clear* north-south differentiation within it as Carr (1938) suggested.[1] I therefore reject *cataspila* Günther 1885 (type locality "Mexico") in favor of *ornata* Gray 1831 (type locality Mazatlan, Sinaloa, Mexico). In thus synonymizing

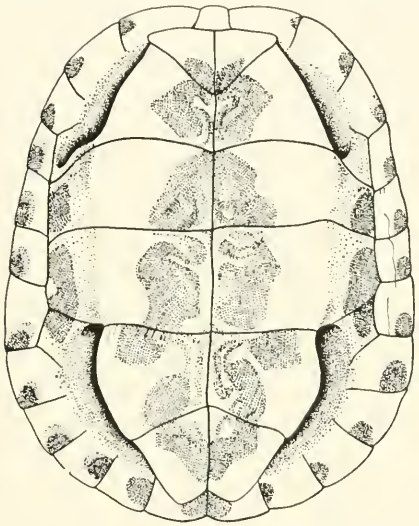


Fig. 3. Plastral pattern in *Pseudemys scripta nebulosa* type. (After Van Denburgh 1895.)

cataspila, I adhere to the philosophy that no infraspecific population should be given a formal latin name unless it is sharply set off by one or more distinctive features that are constant or nearly so within a geographic area the borders of which can be rather sharply defined.

The plastral pattern is one of closed concentric lines sometimes occupying the center of the plastron or sometimes spread out

1 Carr (1938) formed his concept of *cataspila* in part on the specimen made the type of *P. s. gaigeae* by Hartweg (1939a, 1939b).

along the sutures in very complex fashion. There is perhaps a tendency to greater width and complexity of pattern in more southerly localities but the range of variation is extreme; even Costa Rica and Panama individuals may have very narrow plastral figures. Some of a series from Rama River Nicaragua (AMNH 12415-23) show especially wide and elaborate plastral figures; in others of the same series the figure is narrow. Typically from Mexico to Panama there are on the head in the temporal region only narrow yellow lines entering the orbit, but in our Costa Rica locality (Coen Dispensary) there is an expanded supratemporal spot much as in *elegans*. The dorsal pattern is more or less clearly ocellate; whether the ocelli touch or do not touch the posterior margins of the dorsal shields appears to be a purely individual feature.

The impression which these notes give of greater variability in *ornata* than in the previously mentioned populations is probably erroneous. Because these populations approach *callirostris* so closely both geographically and in their characters, I have examined greater numbers of specimens and I am thus more aware of variability. *Ornata* appears to be a set of populations fully as well defined as any other. Intergradation to the north with *gaigeae* and *elegans* appears to be well established (Hamilton, 1947).

8. *Callirostris* in Colombia and Venezuela has the dorsal pattern ocellate like *ornata*, has a plastral figure, whether narrow or wide, of closed concentric lines as in *ornata* and differs from most *ornata* including Panamanian populations in having a reddish supratemporal spot that does not enter the eye, and differs from all other *Pseudemys* in a fully ocellate pattern on the chin and snout. Intergradation with *ornata* in western Colombia is inferred but not demonstrated.

9. No *Pseudemys* is yet known in eastern Venezuela or the Guianas. The only South American population other than *callirostris* (and at the extreme northwest *ornata*) is that in the far south in Rio Grande do Sul, Brasil, and in neighboring parts of Argentina. This is again a member of the *scripta* series but is usually considered a distinct species, *P. dorbigni*. Though separated by half a continent from *callirostris* it shows some decided resemblances to that form. The plastral figure is a broadened intense *ornata*-like figure quite similar to the plastral figures

in Colombian *callirostris*. It is distinctive in the intensity of the black pigmentation rather than in any detail of pattern. The supratemporal stripe is enlarged and separated from the orbit as in *callirostris*. The snout is striped and there is a median stripe forking posteriorly on the chin but at the corners of the lower jaw there is on each side an ocellus not significantly different though perhaps slightly longer than in the *callirostris*. Even the dorsal pattern of the carapace is sometimes ocellate as in *ornata* or in *callirostris*, but here the similarity is verbal rather than exact. The ocellus in *ornata* and *callirostris* is a light ring enclosing a darker central spot. In *dorbigni* the ocellus when present is a transversely elongate ring of black surrounding a very light (in alcohol, white) center. In other specimens the ocellus is drawn out into a transverse streaked pattern.

Pseudemys dorbigni is the terminal member of the continental *scripta* series. There is, however, a subsidiary series in the West Indian islands. I have briefly surveyed this series also and distinguish within it three subgroups with regard to plastral patterns.

1. *Pseudemys decussata* from Cuba, *P. s. stejnegeri* from Puerto Rico, *P. s. vicina* from Hispaniola, though differing each in a minor but characteristic way, all resemble to an amazing degree some specimens of *ornata*, in particular those from Rama River in Nicaragua (AMNH 12415-23) already cited.

2. I have seen only a few specimens of young *P. terrapen*, none of which is fully similar to the *decussata-stejnegeri* subseries. The single MCZ juvenile is quite unique, as compared with all *Pseudemys* that I have examined, in its broad unified black plastral marking. Slightly older specimens at the United States National Museum are more *ornata*-like (probably falling within the variability of *ornata*) but distinctly less complex in pattern than *decussata* and *stejnegeri*. Even the solid pattern of the MCZ juvenile, however, seems best interpreted as a modified *ornata* pattern.

3. Quite isolated in plastral pattern is *P. decorata* (said to occur sympatrically with *P. s. vicina*). In this, there are small light-centered spots on the plastron like those of *elegans* but without the regular arrangement characteristic of *elegans*. This condition is again probably derivable from the *ornata* pattern and probably from the more complex varieties of this by break-

down and diminution of pigment. An occasional specimen of *decussata* approaches *decorata* by the fragmentation and simplification of the plastral pattern but without achieving the scattered ocelli of *decorata*. Some specimens of *decorata* have the plastral ocelli elongate and smudged so as to approach, but at a distance, the plastral pattern of *decussata*.

All three groups of the West Indian *Pseudemys* are otherwise very similar and very like *ornata*. All have an ocellate carapace pattern and striped heads and chins. All, however, tend to have the head striping fainter than in continental forms and all tend to lose at least dorsal pattern early.

It is possible that I have here somewhat oversimplified the picture. Certainly there is much to be done in clarifying the variation within as well as the intergradation between named forms. There are many general statements in the literature regarding intermediates between one or another subspecies usually with remarks on greater similarity to one than to the other. Such statements cannot be independently evaluated until there is more precise information on the characters on which these judgments are made. I have not myself seen the intergrading populations in any of the several cases.

A special problem still remaining is that of *Pseudemys grayi* Bocourt.[1] The United States National Museum has several skulls and shells belonging to this form. The slender skulls look very different from those of *ornata*, but it is not clear to me how the shells of *grayi* are to be separated from those of *ornata*. Carr (1938) has suggested that *P. grayi* may represent only the males of *ornata*, but if so the differences seem both very extreme and highly localized. A biological problem is evidently concealed under the name *P. grayi* which merits more attention than it has received.[2]

However, in spite of unresolved problems, an inspection of *scripta* series as a whole does make it clear that there are several grades of differentiation within it. Morphologically, the major break lies between the populations of the United States, with

1 For the use of *P. grayi* Bocourt rather than *P. umbra* O'Shaughnessy see Mertens and Wermuth (1955).

2 The heads of males of *P. decorata* from Hispaniola and *P. stejnegeri* from Puerto Rico are also strikingly narrow; those of males of *P. decussata* from Cuba are not.

their linear dorsal, and absent or uncomplicated ventral, pattern, and the populations to the South (Mexico, Central and South America and the West Indies), with their ocellate dorsal and typically "ornate" ventral pattern. Possibly the latter is the more primitive. Certainly it is suggestive that the ventral pattern of the *ornata* subseries is substantially identical with a ventral pattern which occurs in the *P. floridana* series (*P. rubriventris* and *P. floridana*) and also in the two genera closely related to *Pseudemys*, *Graptemys* and *Chrysemys* (*C. picta belli*, *C. picta marginata* and *G. pseudogeographica*).

Geographically situated at the major break within the *scripta* series, the populations called *gaigeae*, *nebulosa* and *hiltoni* are in some regards intermediate but appear also to have characters of their own. *Gaigeae* appears to bridge the gap biologically (Hamilton 1947).

In the *scripta* subseries the differences between *elegans* and *scripta* are sharp and constant within the typical areas of these two named populations. *Troosti* as currently restricted (Burger 1952) is a population somewhat intermediate between *scripta* and *elegans*.

In the *ornata* subseries there is a sharp single character difference between *ornata* and *callirostris* and a more complex but less obvious difference between both these and *dorbigni*. Certain of the West Indian forms (*decussata* and *stejnegeri*) differ less from some *ornata* than *ornata* may differ within itself. Yet these forms superficially so close to *ornata* show a probably more meaningful affinity with their more differentiated island neighbors *terrapen* and *decorata*.[1]

The example of the insular forms suggests that caution may be desirable in evaluating degrees of difference on the mainland. While it is clearly possible that all the *scripta* series (*P. decorata* and perhaps *P. grayi* apart) is one species, it is equally clear that the situation is not simple and needs much further *detailed*

1 Mertens and Wermuth (1955 p. 366-367) list all the currently named West Indian forms as subspecies of *terrapen*. While this indicates a relation among these forms which I believe to be real, I do not think it indicates correctly the several grades of this relationship. I do not regard *angusta* and *plana* as recognizable. *Felis* and *malonei* may be neither native nor recognizable, while *granti* may be retained *sub judice*. Tentatively, I suggest the following arrangement: *Pseudemys decussata decussata* (the sole Cuban form), *Pseudemys decussata ricina* (Hispaniolan), *Pseudemys decussata stejnegeri* (Puerto Rican), *Pseudemys decussata granti* (Cayman), *Pseudemys terrapen* (Jamaican), *Pseudemys decorata* (Hispaniolan).

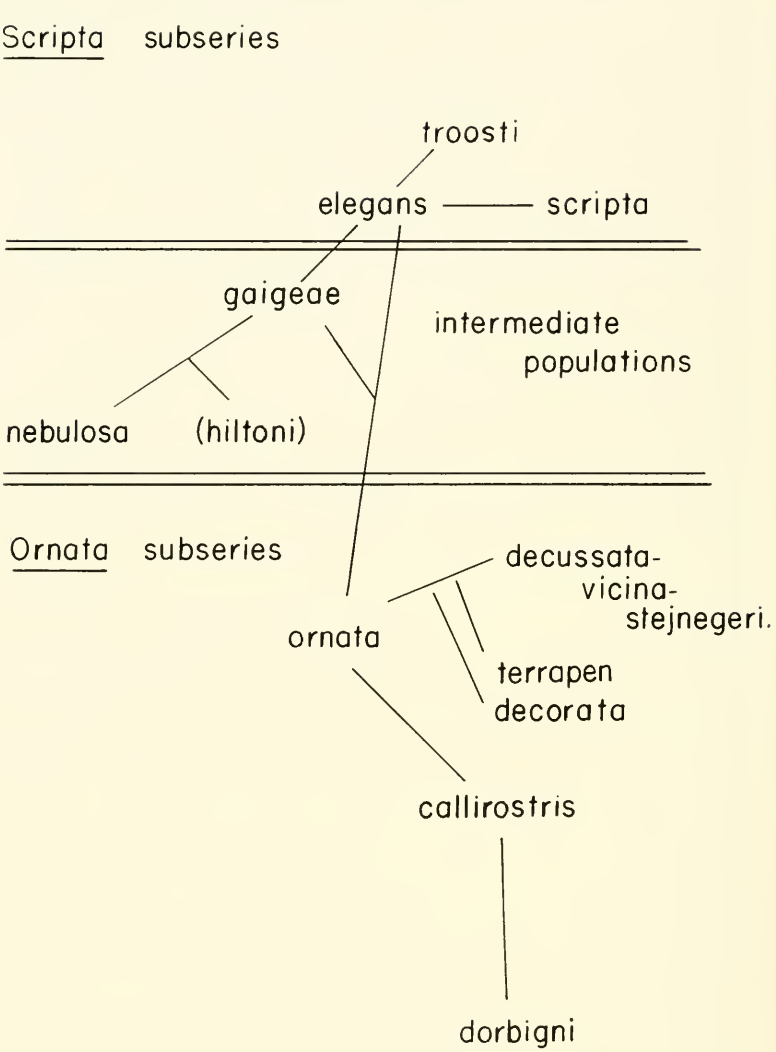


Fig. 4. Diagram to show groupings and approximate geographic position and affinities in the *scripta* series.

study. For my part I am content to modify the current nomenclature of mainland forms to a minimal extent, indicating by the new combination *P. scripta callirostris* that *callirostris* differs only in minor though constant ways from its nearest neighbor in the *scripta* series, *P. scripta ornata*, that these differences seem less than those between populations known to intergrade, and that though there is no present critical evidence of intergradation there are also no counter arguments to the hypothesis of subspecies status.

Acknowledgments: I am indebted to the authorities at the United National Museum, the Philadelphia Academy of Natural Sciences, the Chicago Natural History Museum and the American Museum of Natural History for the privilege of examining their collections. I wish to thank also Mr. Benjamin Shreve, Mr. Arthur Loveridge and Mr. Walter Auffenberg for reading the manuscript and making suggestions.

REFERENCES

Boulenger, G. A.
1889. Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Museum (Natural History). London, 311 pp.

Burger, W. L.
1952. A neglected subspecies of the turtle *Pseudemys scripta*. Jour. Tenn. Acad. Sci., **27**: 75-79.

Carr, A. F.
1938. Notes on the *Pseudemys scripta* complex. Herpetologica, **1**: 131-135.
1942. A new *Pseudemys* from Sonora, Mexico. Amer. Mus. Novitates, No. 1181: 1-2.
1952. Handbook of turtles. The turtles of the United States, Canada and Baja California. Ithaca, N. Y. 542 pp.

Cope, E. D.
1887. Catalogue of the batrachians and reptiles of Central America and Mexico. Bull. U. S. Nat. Mus., **32**: 1-98.

Gray, J. E.
1855. Catalogue of shield reptiles in the collection of the British Museum, Part I. Testudinata. London, 79 pp., 42 plates.

GÜNTHER, A.
1885. Chelonia, *in* Reptilia and Batrachia. Biologia Centrali - Americana, pp. 1-18.

HAMILTON, R. D.
1947. The range of *Pseudemys scripta gaigeae*. Copeia, 1947: 65-66.

HARTWEG, N.
1939a. A new American *Pseudemys*. Occ. Papers Mus. Zool., Univ. Michigan, No. 397: 1-4.
1939b. Further notes on the *Pseudemys scripta complex*. Copeia, 1939: 55.

MERTENS, R.
1952. *Pseudemys callirostris*, eine Schmuck-Schildkröte aus Kolumbien. Aquar-Terrar. Zeitschr., Jahrg. 5: 184-185.

MERTENS, R. and H. WERMUTH
1955. Die rezenten Schildkröten, Krokodile und Brückenechsen. Zool. Jahrb, Syst. Abt., **83:** 323-440.

MULLER, L.
1940. Über *Pseudemys callirostris* (Gray). *In* Tier und Umwelt Südamerika. Ibero-americanische Studien, **13:** 108-126.

RUST, H.
1934. Systematische Liste der lebenden Schildkröten. Blät. Aquar. Terrar., **45:** 42-45, 59-69.

SHREVE, B.
1947. On Venezuelan reptiles and amphibians collected by Dr. H. P. Kugler. Bull. Mus. Comp. Zool., **99:** 519-537.

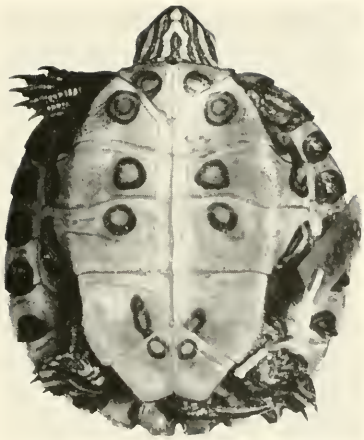
SIEBENROCK, F.
1907. *Chrysemys ornata callirostris* Gray, eine selbstandige Unterart. Zool. Anz., **31:** 790-792.
1909. Synopsis der rezenten Schildkröten mit Berücksichtigung der in historischer Zeit ausgestorbenen Arten. Zool. Jahrb., Suppl., **10:** 427-618.

SMITH, H. and E. H. TAYLOR
1950. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. Bull. U. S. Nat. Mut., **199:** 1-253.

VAN DENBURGH, J.
1895. A review of the herpetology of lower California. Part I. Reptiles. Proc. Calif. Acad. Sci., Sec. 2, **5:** 77-162.

PLATES

Plate 1. Ventral views of turtles of the *scripta* series. Upper left: *Pseudemys scripta elegans* M.C.Z. 12638, Aniston, Alabama. Upper right: *P. s. troosti* M.C.Z. 4905, Knoxville, Tennessee. Lower center: *P. s. gaigeae* M.C.Z. 4551, San Pedro, Mexico.



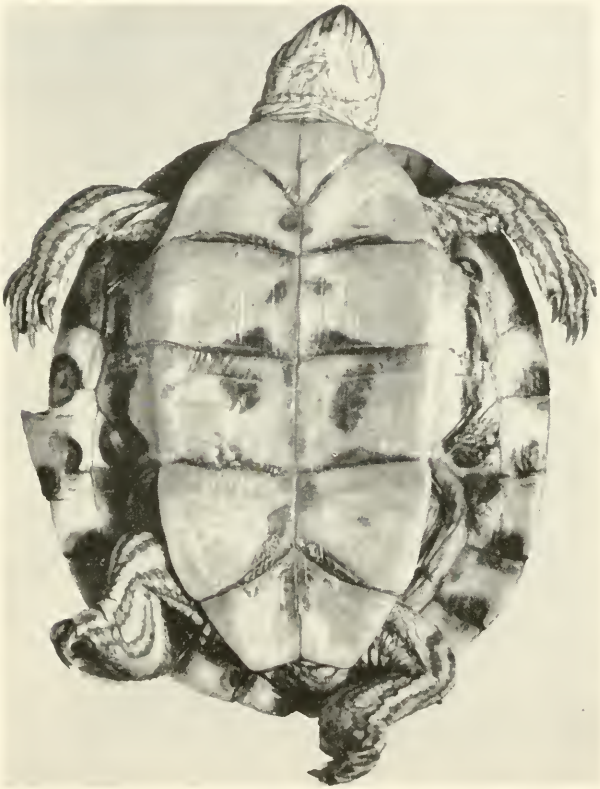
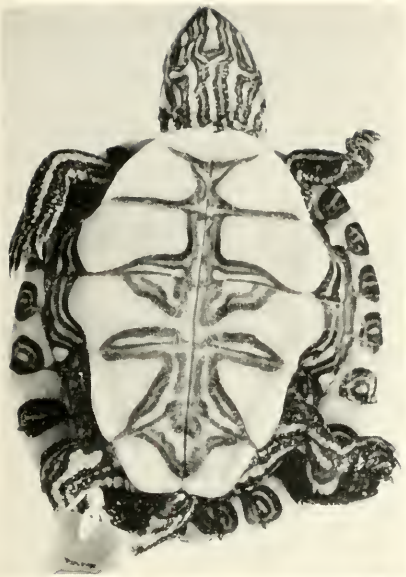


PLATE 1

Plate 2. Ventral views of turtles of the *scripta* series. Upper left: *P. s. ornata* M.C.Z. 19352, Coen Dispensary, Costa Rica. Upper right: *P. dorbigni* M.C.Z. 33502, Porto Alegre, Brasil. Lower center: *P. s. callirostris* M.C.Z. 49055, Cerro Chichiriviche, Silva district, Falcon State, Venezuela.



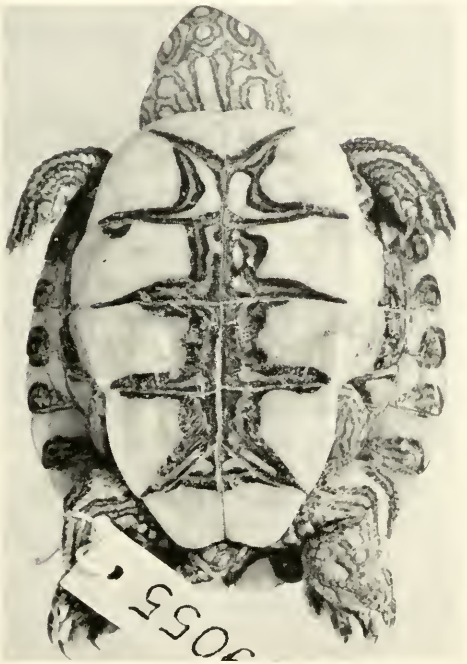


PLATE 2

Plate 3. Ventral views of turtles of the *scripta* series. Upper left: *P. decussata decussata*, M.C.Z. 34179, twelve miles from Soledad, Cuba. Upper right: *P. terrapen* M.C.Z. 52399, Rio Cobre Canal along Spanishtown Road, Jamaica. Lower center: *P. decorata* M.C.Z. 36855, Thomazeau, Haiti.

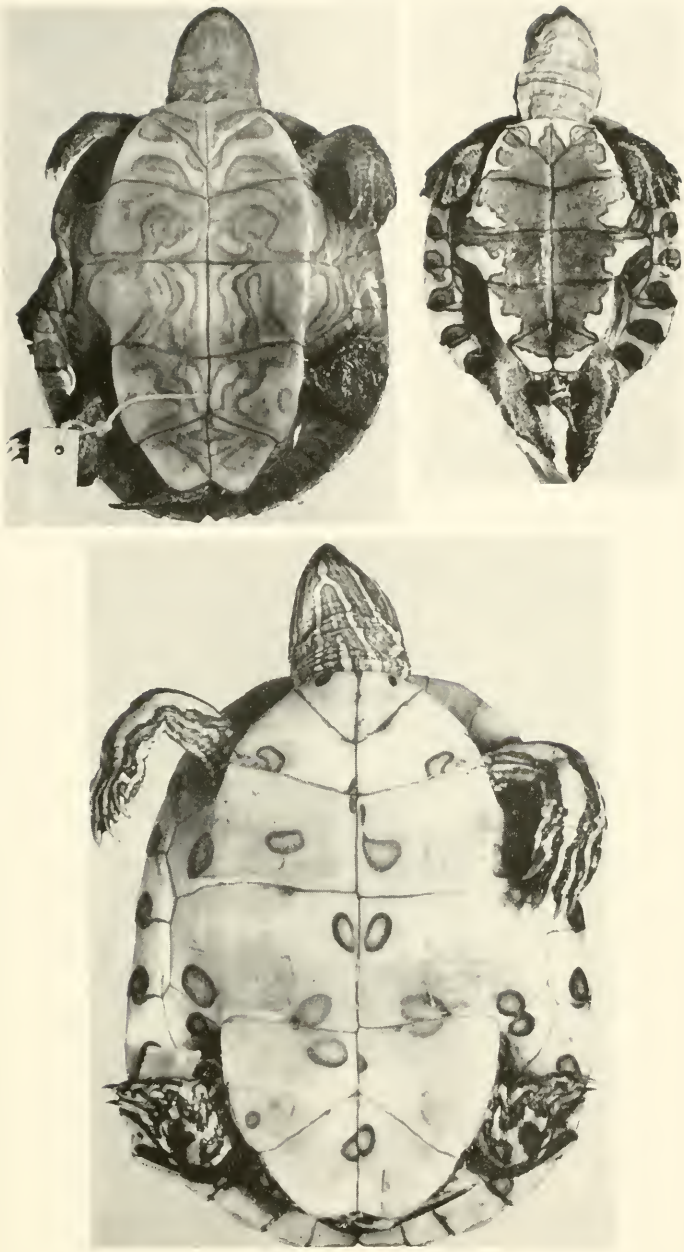


PLATE 3

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 115, No. 6

REVISION OF THE AFRICAN TORTOISES AND TURTLES OF THE SUBORDER CRYPTODIRA

By Arthur Loveridge and Ernest E. Williams

With Eighteen Plates

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

February, 1957

Publications Issued by or in Connection
with the

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 115.

Breviora (octavo) 1952 — No. 61 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 20 is current.

Proceedings of the New England Zoölogical Club (octavo) 1899-1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 6

REVISION OF THE AFRICAN TORTOISES AND TURTLES OF THE SUBORDER CRYPTODIRA

By Arthur Loveridge and Ernest E. Williams

With Eighteen Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
February, 1957

No. 6 — *Revision of the African Tortoises and Turtles of the Suborder Cryptodira*

By Arthur Loveridge and Ernest E. Williams[1]

CONTENTS

	Page
Introduction	163
List of the Cryptodira in Africa	175
List of Keys and Tables	177
Systematic Discussion	180
Bibliography of African Cryptodira	503
Index to All Scientific Names and Synonyms	542

INTRODUCTION

The last comprehensive treatises to embrace all African testudinates were the "Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum," by G. A. Boulenger (1889a), and "Synopsis der rezenten Schildkröten mit Berücksichtigung der in historischer Zeit ausgestorbenen Arten," by F. Siebenrock (1909a).[2] The present contribution is an attempt to bring our knowledge up to date by summarizing all the available information of importance regarding African Cryptodira. This completes the coverage of African Testudinata, as the Pleurodira have already been dealt with by one of us.[3]

Material. We have collaborated in completely rewriting detailed descriptions of the external characteristics of each of the

[1] These names are listed alphabetically, or according to the authors' respective antiquity, without further significance. The entire osteological and paleontological accounts, all major discussions, and the selection of illustrations are the work of my industrious colleague, Dr. E. E. Williams, whose unrivalled knowledge of the Testudinata is well known. Without his erudition and drive, it is safe to say that this monograph would never have been completed in so comprehensive a form. A.L.

[2] Though published on October 31, 1955, the checklist of the turtles of the world by Drs. Mertens and Wermuth, unfortunately did not reach us until the manuscript of this paper had been submitted for publication. It was thus too late for citation under genera and species and should be consulted for the numerous differences.

[3] Loveridge, A., 1941, Bull. Mus. Comp. Zool., 88: 465-524. One of a series of revisionary studies of various families of African reptiles published between 1939 and 1947.

32 species or forms here recognized. In doing so we have been fortunate in having available in the Museum of Comparative Zoology African material of all 32 forms with the exception of one marine species, together with many paratypical or topotypical examples of them or their synonyms.

In order to examine other types, and in search of additional information, one of us (E. E. W.), as a Guggenheim Fellow, spent many months studying testudinates in most of the principal museums of Europe (Leiden; London; Munich; Paris; Frankfurt-am-Main) and eastern North America (Chicago; New York; Philadelphia; Washington). Upon his return, the curators of all these and many other institutions generously loaned for further comparative study much critical material — often of a bulky or fragile nature necessitating careful packing.

When such loaned material is referred to, we have indicated the institution by one of the following abbreviations:

A.M.N.H., American Museum of Natural History, New York.
B.M., British Museum (Natural History), London.
C.M., Carnegie Museum, Pittsburgh.
C.N.H.M., Chicago Natural History Museum, Chicago.
G.M., Museum d'Histoire naturelle, Geneva.
H. M., Zoologisches Museum, Hamburg.
I.F.A.N., Institut Français d'Afrique Noire, Dakar.
L.M., Rijksmuseum van Natuurlijke Historie, Leiden.
M.M., Zoologische Sammlung des Bayerischen Staates, Munich.
P.M., Museum National d'Histoire naturelle, Paris.
N.R., Naturhistoriska Riksmuseum, Stockholm.
S.M., Senckenbergische Naturforschende Gesellschaft, Frankfurt a. M.
T.M., Transvaal Museum, Pretoria.
U.S.N.M., United States National Museum, Washington.
V.M., Naturhistorisches Museum, Vienna.
W.M., Naturwissenschaftliche Sammlung, Neues Museum, Wiesbaden.
Y.P.M., Yale Peabody Museum, New Haven, Connecticut.
Z.M.U., Zoologisches Museum der Universität, Berlin.

Acknowledgements. We herewith welcome this opportunity to express our appreciation for the coöperation of colleagues both here and abroad, especially of those who, with unfailing courtesy, have answered endless questions of a seemingly trivial nature that involved careful examinations of specimens in their charge. We have made exceptionally heavy demands on the

British and Transvaal Museums, whose collections of African Cryptodira are particularly rich.

For lending specimens and/or answering queries we desire to express our grateful thanks to:

V. Aellen (Geneva Museum)
J. C. Battersby (British Museum)
G. Belloc (Institute Oceanographique Monaco)
C. M. Bogert (American Museum of Natural History)
R. D. Brongersma (Leiden Museum)
P. Chabanaud (Paris Museum)
D. M. Cochran (United States National Museum)
J. Eiselt (Vienna Museum)
V. F. FitzSimons (Transvaal Museum)
J. T. Gregory (Peabody Museum, Yale)
J. Guibé (Paris Museum)
F. Heineck (Wiesbaden Museum)
W. Hellmich (Munich Museum)
A. C. Hoffman (Bloemfontein Museum)
R. F. Inger (Chicago Museum)
W. Lanz (Geneva Museum)
R. F. Lawrence (Natal Museum)
M. E. Malan (Stellenbosch University)
R. Mertens (Senckenberg Museum)
B. L. Mitchell (Nyasaland Tsetse Control)
E. Mohr (Hamburg Museum)
C. F. Moysey (Devonshire, England)
F. Neubar (Wiesbaden Museum)
H. W. Parker (British Museum)
J. A. Peters (Brown University)
N. B. Richmond (Carnegie Museum, Pittsburgh)
H. Rendahl (Swedish Museum)
C. A. du Toit (Stellenbosch University)
A. Villiers (I.F.A.N. Museum, Dakar)
H. Wermuth (Zoologische Museum, Berlin)
J. G. Williams (Coryndon Museum, Nairobi)
G. F. de Witte (I.R.S.N. de Belgique)

We also wish to express our appreciation to Mr. Thomas Andersen of Kidugallo, Tanganyika Territory, for endeavoring to obtain for us certain specimens of *Malacochersus;* to W. H. Archer of East London, South Africa, for writing us about *Geochelone;* to G. S. Cansdale of London, England, for answer-

ing questions regarding Gold Coast *Kinixys;* to C. Jacot-Guillarmod of Basutoland, respecting the occurrence in that country of *Psammobates;* to our colleague Dr. Ernst Mayr for advice on various taxonomic enigmas; to T. S. Jones, Esq., of Sierra Leone, for securing specimens that established the presence of *Kinixys b. nogueyi* in that country, and not least to J. M. Savage of University of Southern California for his kindness in reading over, and commenting on, this manuscript.

We welcome this opportunity to acknowledge our indebtedness to the following artists whose numerous drawings add much to the usefulness of this revision: Mr. S. B. McDowell of New York, Miss E. R. Turlington of London, Miss P. M. Washer of the Museum of Comparative Zoology. We are also grateful to Messrs. Peter Green of London, England, and Frank White of Cambridge, Massachusetts, for their photographic achievements, and to the Trustees of the British Museum (Natural History) for permission to reproduce various photographs of specimens in that institution.

Taxonomy. Though, as a result of collaboration, the scope of this revision is greater than that of its predecessors, changes in nomenclature are remarkably few, for we have endeavored to maintain a conservative attitude throughout. The only fresh names proposed are: *Aldabrachelys,* new subgenus for the giant tortoises of Aldabra, etc., *Pseudotestudo,* new subgenus for the dwarf tortoise of Egypt and Libya. No new species or races have been erected, though in certain instances (*Malacochersus, Cyclo-derma*) the possibility of their existence has been noted.

At the specific and infraspecific level emphasis has been rather on the suppression of names, never lightly or on theoretical grounds, but only after a careful examination of the available material failed to support their claims to specific or racial distinction. In some cases (such as *Kinixys belliana*) the accumulation of additional tortoises may produce valid reasons for the revival of forms we have not recognized. But to sustain these names will require more comprehensive and careful studies than those on the basis of which they were proposed. It cannot be too strongly emphasized that testudinates should never be described on single characters and but rarely on a single specimen. Conclusions based on series that are limited to less than ten

individuals should be viewed with suspicion, for it is highly probable that the apparently constant characters displayed by so small a sample will prove to be unstable when a larger series is available.

The status of one species, *Cyclanorbis elegans* Gray, founded on a juvenile, has been clarified by synonymizing with it *oligotylus* Siebenrock, founded upon an adult.

At the generic level the changes recommended,[1] though not minor, are infrequent. Thus, after a careful survey which included consideration of extra-limital forms, we have concurred with present South African usage in recognizing the large tortoises of Africa as generically separable from *Testudo, sensu stricto,* as are also the members of the *geometricus* group and *angulata* (for details cf. pp. 218ff). Another change in the concept of a genus has necessitated our removing the North American pond-turtle species *blandingii* to the genus *Emydoidea,* retaining in *Emys* only the species *orbicularis* of Europe and Africa.

At every point in our taxonomic study we have been faced with the fact that in *all* characters the amount of variation exhibited by members of this order is frequently astonishing and always disconcerting. In our descriptions of external characters we have endeavored to record every major variation encountered. The number of such observed variations, it should be noted, is apt to bear a direct ratio to the number of specimens studied. Thus, where relatively large series were available to us, as in the case of *Geochelone p. babcocki, Malacochersus tornieri* or *Kinixys b. belliana,* our earlier crude observations were constantly subjected to qualifying comment. If we have used such words as "always" or "never" anywhere in the descriptions, it has been in a moment of unguarded enthusiasm.

This high degree of variability extends to osteology also. There are no grounds for assuming that internal characters are more constant than external ones. The only certain test of stability for both is the empirical one of examining a large series. Here a practical difficulty arises, as series of skeletons are rarely available. Since, with good reason, generic definitions are largely

[1] See also footnote on p. 220.

based on osteological characters, the lack of skeletal series has been a real handicap.

In this predicament our method has been to rely upon determination of the range of variation in a test species, *Geochelone pardalis babcocki,* for which numbers of skulls and skeletons were available. Whatever species, judged by even a few specimens, lay wholly outside the variation of this form in several major skeletal characters (e.g. maxillary ridging, pygal number, neural shape, etc.) could, we felt, be safely regarded as only remotely related and hence possibly generically distinct. However, we have not been content with this estimate of morphological distance only, but wherever possible have endeavored to trace lineages in the fossil record. We have accepted paleontological evidence as constituting additional osteological material, and where the separation of lineages proved to be of great antiquity — as, for example, going back to the Eocene — accepted it also as modest warranty of generic distinction.

While availing ourselves of published descriptions and illustrations, our first assessment of the degree of osteological variation in any given species or genus has been based on specimens we ourselves have examined. Thus of the 27 African terrestrial or freshwater species dealt with in this study, we have seen skeletal material of all except three, viz. *Psammobates geometricus, Homopus signatus* and *H. femoralis.* Of certain other species relatively little material (less than three skulls or skeletons) has been available: only single skulls of *Geochelone sulcata, Psammobates oculifer, Homopus boulengeri* and *Cycloderma aubryi.* On the other hand, our understanding of the African species and our ideas as to the variational range within their subfamilies and families have benefited by the examination of much extralimital material including, for example, both skulls and skeletons of most of the species and every species-group of the Testudininae.

Categories at every taxonomic level need to be studied against a background of the next higher category if they are to be fully understood. Thus no subspecies can be properly evaluated without a reasonably adequate knowledge of the entire species of which it forms a part. No species can be appreciated without a substantial acquaintance with the whole genus in which it is

included. No genus can be satisfactorily defined except in terms of full information of at least the section of the subfamily to which it is assigned. Consequently we have not hesitated to explore — for their background value — extralimital forms and problems whenever these seemed likely to shed significant light on their African counterparts. It is on this account that family or subfamily phylogenies have been included, together with discussions of non-African genera or species, and even definitions of certain extralimital forms.

Despite all our care, our definitions, whether specific, generic or familial, are weakened, at least in appearance, by the fantastic variability on which we have commented above. Our key to the external characters of families mentions lack of horny scutes in a solitary sea turtle. On another occasion one of us (Williams, 1954, Breviora, No. 29) has called attention to variation in a "family character" of an African pleurodire species. Such radical variations cannot in honesty be omitted from the record, but it is important to recognize that *they do not actually diminish the value as phyletic units of the categories whose "definitions" they disturb.* However, they do show how necessary it is to use the greatest care and the most broadly based knowledge in dealing with the vexing problem of the recognition of natural groups. Some aspects of these matters have been discussed in very percipient fashion by Zangerl and Turnbull (1955, Fieldiana: Zoology, **37**:366 ff.)

At the outset, the idea occurred to us to include under each species a synopsis of any *Problems remaining,* or gaps in the life-history requiring to be filled. However, we soon realized that such synopses would be unavoidably repetitious and much too long. Perhaps the most fully documented form is the Eastern Leopard Tortoise (*Geochelone pardalis babcocki*), but no African cryptodiran can be said to be well known. One has only to refer to the various headings given under each species or race to realize how very sketchy is our knowledge of their respective ecologies, dietetic preferences, reproductive habits, geographic variation and range.

In the case of *Anatomy* the information was in general so scanty that this heading was also omitted throughout, though references to anatomical papers are retained in the citations for

each species. Only once has the anatomy of an African species been studied adequately, and this was done on non-African material. We refer to the very old but classic work of Bojanus (1819-1821) on *Emys orbicularis*. Less meritorious, but possibly based on African specimens, at least in part, is that of Thomson (1932) on "the Tortoise" (i.e. "*Testudo graeca*" = *hermanni*, and "*Testudo ibera*" = *graeca*). Other anatomical discussions involving African turtles either mention African forms incidentally or in a more general context (e.g. sundry papers by Siebenrock), or else record anatomical observations of no great scope.

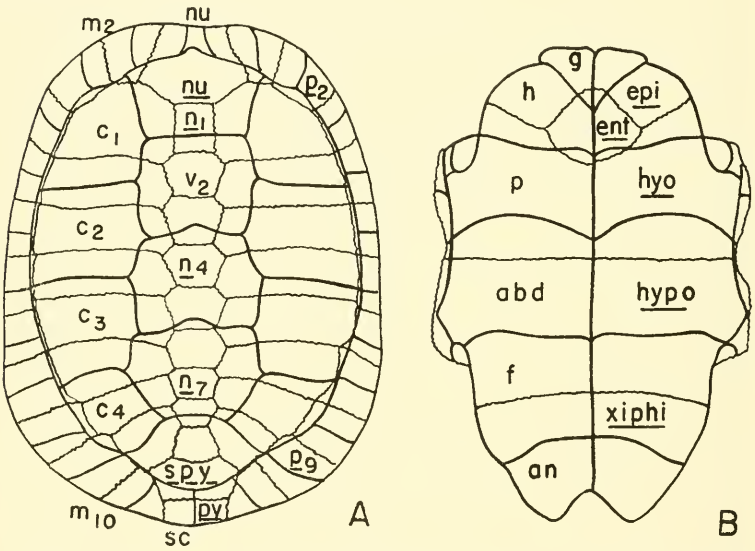


Fig. 1. *Clemmys caspica leprosa:* diagram of shell to show nomenclature of horny scutes and bony plates, the latter's abbreviations underlined in the figure and italicized below. *A*, Carapace: c 1-4 = costals; m 2, 10 = second and tenth marginals; *n* 1-7 = neurals; nu = nuchal scute; *nu* = nuchal bone; *p* 2, 9 = second and ninth peripherals; *py* = pygal; spy = suprapygal; v 2 = second vertebral. *B*, Plastron; abd = abdominal; an = anal; *ent* = entoplastron; *epi* = epiplastron; f = femoral; g = gular; h = humeral; *hyo* = hyoplastron; *hypo* = hypoplastron; p = pectoral; *xiphi* = xiphiplastron.

(P. Washer del.)

Terminology. We have introduced no new terms or new usages to the nomenclature of either bones or horny shields. For the dorsal shell our usage is that of George Baur in his several papers, differing from that of Boulenger only by distinguishing the rib-containing bony plates as "pleurals," and the bones surrounding the shell as "peripherals." Our nomenclature for the dorsal shell is contrasted with that of other authors in Table I (see also Fig. 1).

Fortunately there has never been any confusion with regard to the names of either the bones or horny shields of the ventral shell. To express length-relationship between the various plastral shields we have introduced a new "plastral formula" in which the shields are listed in order from longest to shortest. This formulation is not a substitute for precise studies of the length ratios between plastral shields, but, despite variability, it tends to be characteristic of species, genera, and occasionally of even

TABLE 1

Nomenclature of the parts of a turtle shell

HORNY SHIELDS

Our usage	Boulenger 1889	Hay 1908	Carr 1952
nuchal	nuchal	nuchal	precentral
vertebral	vertebral	vertebral	central
supracaudal	supracaudal	supracaudal	postcentral
costal	costal	costal	lateral
marginal	marginal	marginal	marginal

BONES

Our usage	Boulenger 1889	Hay 1908	Carr 1952
nuchal	nuchal	nuchal	proneural[1]
neural	neural	neural	neural
suprapygal	pygal	suprapygal	epipygal
pygal	pygal	pygal	pygal
pleural	costal	costal	pleural
peripheral	marginal	peripheral	peripheral

1 Though, by the invention of this and other novelties, Carr intended his terminology to reduce confusion, here it is definitely at fault. The very similar term "preneural" has long been in use for an element that is immediately posterior to the nuchal of authors in certain Asiatic and fossil trionychids and some other fossils.

higher units. Thus a plastral formula[1] with Abd>h> (all other elements), or with Abd> (all other elements) turns out to be very characteristic of testudinines.

As for head shields in the testudinines, we have adopted the terms used by Miss Procter for *Malacochersus tornieri*. In this species, as also in the members of the genus *Testudo*, the dorsal aspect of the head possesses the most elaborate regular scutellation to be found in tortoises. The terms employed are "supranasals," "prefrontals" and "frontals." With regard to the still more elaborate head scutellation of the marine turtles, we follow Deraniyagala (1939:192:fig. 76) except in employing the term "supratemporals" for what he calls "temporals," as being more appropriate.

Folklore. Probably few reptiles figure so frequently in African folk tales as do tortoises. All manner of superstitions are entertained concerning them, and references to such beliefs constantly crop up in books of travel by the earlier explorers. As we came across relatively few examples in our search of zoological papers we have omitted the subject altogether, rather than treat it inadequately. The matter merits the attention of some anthropologist who, preferably in collaboration with a zoologist, would scan the literature and publish a classified synopsis of these tales and beliefs.

Citations. Following the name of each species, when used as a heading, citations to it or its synonyms are given in an abbreviated form which can be amplified by reference to the Bibliography on p. 503. Almost 550 papers (1758-1955) in which we have found references to African Cryptodira are listed. Omitted from the bibliography are papers involving some single generic or specific description for which an adequate citation has already been given in the synonymy. Also omitted are citations to non-African species or races mentioned in the text; these are given in parentheses or as footnotes.

Attention is directed to the Synopsis Methodica (a folding chart or table in which binomials are employed) at the end of the first volume of Lacépède, 1788 "Histoire naturelle des Quadrupèdes ovipares et des Serpens," a work frequently rejected by systematists since only popular names are employed in the text.

[1] See Fig. 1 for significance of abbreviations.

An extraordinary volume that cannot be taken seriously, is that of Rochebrune, 1884a, "Faune de la Sénégambie. Reptiles." In it the author lists as occurring in Senegal such impossibilities as *Testudo marginata, T. geometrica, Homopus signatus, H. areolatus* and *Cycloderma frenatum.* Despite the fact that definite Senegambian localities are furnished for them, only four, or at most five, of the eighteen land and freshwater turtles listed by Rochebrune actually occur in Senegal.

A question arises with regard to the priority of J. E. Gray's contributions cited as 1831b and 1831c. The latter — Synopsis Reptilium — contains many original descriptions and was clearly intended to be published first. Unfortunately, the evidence suggests that 1831b — Synopsis of the Species of the Class Reptilia — which appears as an appendix to Edward Griffith's translation of Cuvier's Animal Kingdom, came out first. In Gray's own bibliography the date is given as 1830; this is possibly the date of its completion, an advance copy, or an earlier edition than the usually accepted one of 1831. This synopsis in Griffith makes only passing reference to, or gives the scantiest descriptions of, species more fully dealt with in 1831c. For this reason, whenever a new species is involved, we have cited 1831c in advance of 1831b. In no case does it affect priority of nomenclature.

In listing a reference to some form, we do not intend to infer that the *entire synonymy* of the author cited necessarily applies to the species or race to which it is assigned.

Localities. It will be noted that localities are listed alphabetically under their respective countries. The latter, beginning with Morocco, are arranged clockwise around the continent. The only exception to this is in the case of trionychids from north of the equator, whose ranges are given from the Nile west to Senegal. Generally speaking, we have adopted the orthography of the government administering the area, though a few exceptions such as Algiers (instead of Alger), and Tangiers (in lieu of Tanger), have been allowed to stand. Where the current spelling of a place name differs from that used in the original record given in the literature, the rejected spelling is given in parenthesis after the preferred one.

A locality preceded by an asterisk implies that a specimen from the place in question has been studied by us; usually it is in the Museum of Comparative Zoology. If it is in some other institution, however, the key letters of the museum where it is preserved follow the locality in parenthesis. In many instances such asterisk-bearing localities constitute fresh records of occurrence for the species and will not be found in the literature.

A locality that appears in quotation marks is one that has been taken from the literature but which we have failed to find on any map. In some instances, at least, the name may have been misspelled or misprinted.

Unfortunately, all localities appearing in the literature cannot be accepted. The handsome and ornate shells of tortoises have attracted the attention of mankind from earliest times. This is especially true in South Africa where primitive tribes were accustomed to wear the shells of the smaller species as ornaments, or used them as scoops or receptacles, especially for *buchu* ointment (cf. *Psammobates geometricus* under the heading *Enemies*). Doubtless they were used in barter and, passing from one itinerant African to another, were transported far from their place of origin. In due course some were seen and purchased by European travellers, especially those bent on acquiring objects of anthropological interest. Naturally the shells were labeled as coming from the place where purchased.

In recent times car drivers are likely to stop and pick up any small tortoises encountered wandering on the road. After being transported great distances the reptiles may escape, be liberated, or handed over to whoever happens to put the driver up for the night. All localities that appear questionable are either mentioned in footnotes or at the end of the section dealing with the *Range* of the species in question.

For the convenience of those who wish to see at a glance what species are currently known to occur in a particular country, a chart is provided (p. 179). In general the name of the country only is given, but the Union of South Africa covers so vast an area that its component divisions (e.g. Transvaal, Natal, etc.) have been cited. Similarly, though not invariably, French Equatorial and West Africa have been listed under their major territories (e.g. Gabon, Senegal, etc.) when this appeared advisable.

List of the CRYPTODIRA in Africa[1]

PAGE

Order TESTUDINATA

Suborder CRYPTODIRA 180

Family TESTUDINIDAE 181

Subfamily [PLATYSTERNINAE] 182

Subfamily EMYDINAE 183

Genus [*Emydoidea* Gray] 189

Genus *Clemmys* Ritgen 191

C. caspica leprosa (Schweigger) 192

Genus *Emys* Duméril 201

E. orbicularis (Linnaeus) 202

Subfamily TESTUDININAE 209

Genus *Geochelone* Fitzinger 221

Subgenus *Aldabrachelys* new 225

Subgenus *Geochelone* Fitzinger 225

G. sulcata (Miller) 230

G. pardalis babcocki (Loveridge) 235

G. pardalis pardalis (Bell) 251

Genus *Testudo* Linnaeus 254

Subgenus *Testudo* Linnaeus 261

T. graeca graeca Linnaeus 261

Subgenus *Pseudotestudo* new 276

T. kleinmanni Lortet 276

Genus *Malacochersus* Lindholm 283

M. tornieri (Siebenrock) 286

1 Names in square brackets are those of non-African groups which had to be defined or discussed for taxonomic reasons.

Genus *Psammobates* Fitzinger 294
P. oculifer (Kuhl) 315
P. geometricus (Linnaeus) 319
P. tentorius verroxii (Smith) 324
P. tentorius trimeni (Boulenger) 333
P. tentorius tentorius (Bell) 336
Genus *Chersina* Lindholm 342
C. angulata (Schweigger) 345
Genus *Homopus* Duméril and Bibron 352
H. signatus (Schoepff) 359
H. boulengeri Duerden 362
H. femoralis Boulenger 365
H. areolatus (Thunberg) 367
Genus *Kinixys* Bell 374
K. belliana belliana Gray 384
K. belliana nogueyi (Lataste) 396
K. homeana Bell 400
K. erosa (Schweigger) 404
Family TRIONYCHIDAE 412
Genus *Trionyx* Geoffroy 420
T. triunguis (Forskål) 423
Genus *Cyclanorbis* Gray 436
C. elegans Gray 438
C. senegalensis (Duméril and Bibron) 443
C. sp. 450
Genus *Cycloderma* Peters 451
C. aubryi (Duméril) 453

C. frenatum Peters 459
Family CHELONIIDAE 472
Genus *Chelonia* Brongniart 472
C. mydas (Linnaeus) 474
Genus *Eretmochelys* Fitzinger 484
E. imbricata (Linnaeus) 485
Genus *Caretta* Rafinesque 489
C. caretta (Linnaeus) 490
Genus *Lepidochelys* Fitzinger 494
L. olivacea olivacea (Eschscholtz) 495
Family DERMOCHELYIDAE 498
Genus *Dermochelys* Blainville 499
D. coriacea (Linnaeus) 499

LIST OF KEYS AND TABLES

Key to the Families of Cryptodira in Africa 180
" " " Subfamilies of Testudinidae in Africa 182
" " " Emydinae in Africa 190
" " " Forms of *Clemmys caspica* 192
" " " Genera of Testudininae in Africa 220
" " " Species and Subspecies of *Geochelone* in Africa 229
" " " Subgenera of *Testudo* 258
" " " Circum-Mediterranean Species of *Testudo* 260
" " " Species and Subspecies of *Psammobates* 314
" " " Species of *Homopus* 358
" " " Species and Subspecies of *Kinixys* 383
" " " Trionychidae of Africa 419
" " " Marine Turtles Breeding in Africa 471

PAGE

Table 1. Nomenclature of the Parts of a Turtle Shell 171

Table 2. Recorded Distribution of African Cryptodira 179

Table 3. Characters of the Subgenera of *Geochelone* 223

Table 4. Characters of the African Species and Subspecies of *Geochelone* 228

Table 5. Chronological List of the Specific and Subspecific Names Proposed in *Psammobates* 301

Table 6. Resemblances of *Chersina* to other Genera 343

Table 7. Characters of the Species of *Kinixys* 383

Table 8. Characters of the Two Sections of the Family Trionychidae .. 414

Table 9. Characters of the African Species of Trionychidae 419

Table 10. Marine Turtles Caught on the Senegal Coast 469

Recorded distribution of African Cryptodira around that continent

	Clemmys c. leprosa	Emys orbicularis	Geochelone sulcata	Geochelone p. babcocki	Geochelone p. pardalis	Testudo g. graeca	Testudo kleinmanni	Malacochersus tornieri	Psammobates oculifer	Psammobates geometricus	Psammobates t. verroxii	Psammobates t. trimeni	Psammobates t. tentorius	Chersina angulata	Homopus signatus	Homopus boulengeri	Homopus femoralis	Homopus areolatus	Kinixys b. belliana	Kinixys b. nogueyi	Kinixys homeana	Kinixys erosa	Trionyx triunguis	Cyclanorbis elegans	Cyclanorbis senegalensis	Cycloderma aubryi	Cycloderma frenatum	Chelonia mydas	Eretmochelys imbricata	Lepidochelys o. olivacea	Caretta caretta	Dermochelys coriacea
Rio de Oro																															•	
Spanish Morocco	•				•																											
French Morocco	•	•			•																										•	
Algeria	•	•			•																										•	•
Tunisia	•	•			•																										•	•
Libya (Tripoli etc.)	•				•	•																										
Egypt						•																•					•	•	?	•	•
Sudan			•	•															•			•	•	•							
Eritrea			•																•			•						•	•		
Ethiopia			•	•															•			•									
•French Somaliland																																
British Somaliland				•															•													
Somalia				•															•			•						•				
Sokotra Island																												•	•	•	•	
Uganda Protectorate				•															•			•	•									
Kenya Colony				•				•											•			•						•	•		•	?
Tanganyika Territory				•				•											•									•	•	•	•	
•Pemba Island																																
Zanzibar Island																			•									•	•			
Mafia Island																			•													
Mozambique				•															•									•	•	•	•	
Nyasaland				•															•									•				
Northern Rhodesia				•															•									?				
Southern Rhodesia				•															•													
Bechuanaland Protectorate				•					•										•													
Union of South Africa																																
(Transvaal)				•					•										•													
(Natal)				•															•													
(Orange Free State)									•		•						•															
•Basutoland																																
(Cape Province)				•	?				•	•	•	•	•	•	•	•	•	•										•	•	•	•	•
South-West Africa				•	•				•		•	•		?	•	?															•	•
•St. Helena Island																																
Ascension Island																												•	•		•	
Angola				•															•				•					•				
Cabinda																						•	•			•		•				
Belgian Congo																			•		•	•	•			•		•		•	•	
•Belgian Ruanda-Urundi																																
French Equatorial Africa																				•	•	•		•	•			•	•	•	•	•
Rio Muni																				•	•											
•Annobom Island																																
São Thomé Island																												•	•			
Principe Island																												•	•			
•Fernando Po Island																																
French Cameroon																			•	•	•	•	•	•		•			•			
British Cameroon																				•	•	•								•		
Nigeria			•																	•	•			•	•							
Dahomey																				•												
Togo																				•			•	•	•							•
Gold Coast																				•	•	•	•						•	•	•	•
Ivory Coast																					•	•									•	
Liberia																					•	•	•						•	•	•	•
Sierra Leone																				•		•	•							•		
French Guinea																				•												?
Portuguese Guinea																				•			•						•			
Gambia	•																			•		•	•		•							
Senegal			•																	•			•		•				•	•	•	•
French West Africa	•		•																	•			•									
Cape Verde Islands																													•	•		•
Canary Islands																													•			•
Madeira Islands																																•

* No records known to us

TABLE 2

SYSTEMATIC DISCUSSION

Suborder CRYPTODIRA

1870. *Cryptodira* Cope (part), Proc. Amer. Assoc. Adv. Sci., **19**:235.

Definition. Skull with temporal region frequently emarginate behind; parietal usually not in contact with squamosal; nasals rarely, and lacrimals never, present; prefrontals almost always joining vomer; epipterygoids usually present; pterygoids without lateral rolled-up expansions, always excluding basisphenoid from quadrate; quadrate never enclosing eustachian tube; articular region of mandible concave; splenial rudimentary or absent; dentaries always united.

Head withdrawn by a vertical flexure of the neck; atlas rarely fused to odontoid; cervical vertebrae with rudimentary transverse processes situated anteriorly; posterior cervical spines low; cervical postzygapophyses widely separated; central cervical articulations well developed, posteriorly broad and (usually) double; sacral ribs well developed; pelvis never ankylosed to carapace or plastron; caudal vertebrae usually procoelous.

Shell primitively complete (except for the always absent mesoplastra), variably reduced or its elements lost in specialized forms; horny shields present or absent; if absent, an epithecal component of the bony shell greatly developed.

Key to the Families of Cryptodira in Africa

(Based on external characters)

1. Limbs not modified as flippers, each with 3, 4 or 5 claws 2
   Limbs modified as flippers, with 0, 1 or 2 claws 3
2. Carapace with horny shields; feet with 4 or 5 claws..TESTUDINIDAE (p. 181)
   Carapace without horny shields; feet wtih 3 claws ..TRIONYCHIDAE (p. 412)
3. Carapace with large horny shields;[1] flippers with 1 or 2 claws ..... CHELONIIDAE (p. 472)
   Carapace without large horny shields; flippers clawless DERMOCHELYIDAE (p. 498)

[1] Shields were absent on a single aberrant adult *Chelonia mydas* captured at Karaduva Island (13.xi.1928) where it was examined, while still alive, by Deraniyagala (1939: 227).

Family TESTUDINIDAE

1825. *Testudinidae* Gray, Ann. Philos. (2), **10**:210.

Definition. Cryptodirous testudinates, semi- or fully aquatic or terrestrial in habit. Horny shields always present; costal scutes almost always 4 pairs; marginals exclusive of the nuchal and supracaudal, usually 11 pairs; inframarginals complete or reduced to axillary and inguinal scutes; plastron with 6 pairs of scutes; normally no intergulars.

Skull without nasal bones; prefrontals always in contact dorsally, with descending processes that may be scarcely or widely separated inferiorly; parietal never meeting squamosal; either postorbital or quadratojugal sometimes absent; temporal region posteriorly emarginate or not; quadrate enclosing or not enclosing stapes; post-otic antrum well developed; upper jaw frequently with one or more ridges on its triturating surfaces; vomer always present, separating palatines; mandible with well-developed coronoid bone.

Neck vertebrae usually with 2 biconvex centra, typically the eighth centrum doubly convex in front; coracoids with median borders narrow or markedly widened; tuberosities of humerus widely separated to closely approximated; trochanteric fossa of femur tending to be reduced; phalanges with condyles; claws normally 4 or 5.

Carapace without epithecal component, united to plastron by suture or ligament; sometimes either carapace or plastron with more or less of a hinge; nuchal without well-developed costiform processes; typically peripheral and pleural bones solidly united; neural bones variably shaped; pygals usually 3; plastron never cruciform, usually without fontanelles in adults (except in *Malacochersus*); entoplastron always present; buttresses very strong to absent.

Range. World-wide except for the Australian region.

Remarks. The conception of the TESTUDINIDAE to which we have adhered is that of Williams (1950), in which the family includes the Platysterninae together with the Emydinae and Testudininae. Though only two of these subfamilies occur in Africa, the family definition has been phrased so as to embrace the genus *Platysternon* and the definitions of Emydinae and Testudininae drafted so as to afford contrasts with that Asiatic

genus. In order to clarify the statement of some of the characters cited, it has seemed advisable to present, in addition to the diagnoses of the African subfamilies, one of the Platysterninae also.

Subfamily PLATYSTERNINAE

1950. *Platysterninae* Williams, Bull. Amer. Mus. Nat. Hist., **94**:513, 556.

Definition. Aquatic terrapins. Skin of head undivided; scales on forelimb neither spurlike nor with dermal ossifications; small spurlike tubercles on hinder side of thigh; scent glands present; bursae anales present.

Skull with prefrontals whose descending processes are closely approximated inferiorly; frontal excluded from orbit; postorbital enormously developed, largely covering temporal region; temporal region posteriorly but very slightly emarginate; temporal arcade very solidly constructed; quadratojugal large, in contact with the maxilla; jugal not entering orbit, surrounded by other bones; quadrate not enclosing stapes; surangular largely covered by dentary, only narrowly exposed laterally.

Coracoids with narrow medial borders; tuberosities of humerus widely separated; trochanteric fossa of femur widely open; epipodials moderate; second and third digits always have 3 phalanges.

Carapace very low; rib heads stout, well developed; neural bones rather quadrate; inframarginal series of scutes complete.

Range. Southeastern Asia.

Key to the Subfamilies of Testudinidae in Africa

Skin of head smooth and undivided; digits fully webbed, the second and third with 3 phalanges. Range: ponds and streams of northwest Africa ..... EMYDINAE (p. 183)

Skin of head divided into larger or smaller shields; digits not webbed, the second and third with only 2 phalanges. Range: all of Africa in suitable areas .. TESTUDININAE (p. 209)

Subfamily EMYDINAE

1909. *Emydinae* Siebenrock, Zool. Jahrb. Syst., Suppl., **10**:451.

Definition. Testudinid terrapins of aquatic to fully terrestrial habits. Skin of head entirely smooth or posteriorly divided into small shields; scales on forelimb sometimes bandlike, never spurlike or with osteoderms; spurlike tubercles on hinder side of thigh absent or very small; scent glands present; bursae anales present, occasionally rudimentary.[1]

Skull with prefrontals whose descending processes are typically very closely approximated inferiorly, at most only moderately separated; frontal often entering orbit, sometimes entering temporal fenestra; postorbital typically well developed, never absent; temporal region posteriorly always emarginate; temporal arcade sometimes interrupted by reduction or absence of the quadratojugal; quadratojugal tending to be reduced or absent; quadratojugal and maxilla rarely in contact; quadrate usually not enclosing stapes; surangular largely covered by dentary, only narrowly exposed laterally.

Coracoids with narrow medial borders; tuberosities of humerus usually widely separated; trochanteric fossa of femur usually widely open, except in the more terrestrial forms where it tends to be narrowed or reduced; epipodials moderately elongate; second and third digits always with 3 phalanges, except on the forefeet of the American genus *Terrapene*, where there are only 2, as in tortoises.

Carapace usually low arched; rib heads typically well developed, sometimes much elongated; neural bones primitively hexagonal, short-sided anteriorly, sometimes short-sided posteriorly, rarely octagonal, never vestigial; of the inframarginal series only the axillaries and inguinals normally present.

Range. North and South America; Europe; Asia; North Africa. Absent from tropical and South Africa and the Australian region.

Fossil record. Throughout Cenozoic of North America, Europe and Asia; first reported in the Pliocene of Africa; not known fossil in South America.

1 Bursae anales were not found in *Cyclemys* (= *Pyxidea*) *mouhoti* by J. Anderson, 1876, Jour. Linn. Soc., **12**: 434-444.

Remarks. Only two emydine genera occur in Africa. A study of the African testudinid fauna is, therefore, not an appropriate place for a revision of emydine genera. Nevertheless we have become involved in the problem of their definition and grouping since the distribution of one of the African genera (*Emys*), as currently understood, includes a species (*orbicularis*) from North Africa, Europe, and neighbouring portions of Asia, and a second (*blandingii*) in eastern North America. An investigation of the evidence for this peculiar distribution has convinced one of us (E.E.W.) that the two species are not congeneric.

The basic reasons for this decision were in fact stated by Baur in 1889 (Amer. Nat. **23:** 1099-1100), and will become evident to anyone who studies *skeletons* of *Deirochelys reticularia, "Emys" blandingii* and *Emys orbicularis.*

A decision of this sort involves a sorting out of convergent and phylogenetically meaningful characters. It is best done in a frame of reference that includes a conception of the relationships of all emydine genera. Figure 2 is an attempt to provide this appropriate background. The scheme given there is tentative; it is not a phylogeny since it neglects the temporal dimension and omits all fossil forms (disregarded for this subfamily, as they are poorly known and worse analysed). However, the diagram, wherever it indicates the direct derivation of one genus from another does predict that the actual ancestral fossil will "key" out very near the living genus which has been given the more central and thus "primitive" position.

In Figure 2 we have postulated an unknown (presumably Asiatic) ancestral emydine, inferring as the characters of this hypothetical animal those which would most closely approach the characters found in related and primitive families (estimating primitiveness from the characters held in common by the older fossil families). On this basis we consider that the ancestral emydine had:

1. a carapace with surface sculpture;
2. a skull with a strong temporal arcade;
3. moderate axillary and inguinal buttresses;
4. maxillae with rather wide triturating surfaces but no secondary palate;
5. quadrate not enclosing the stapes;

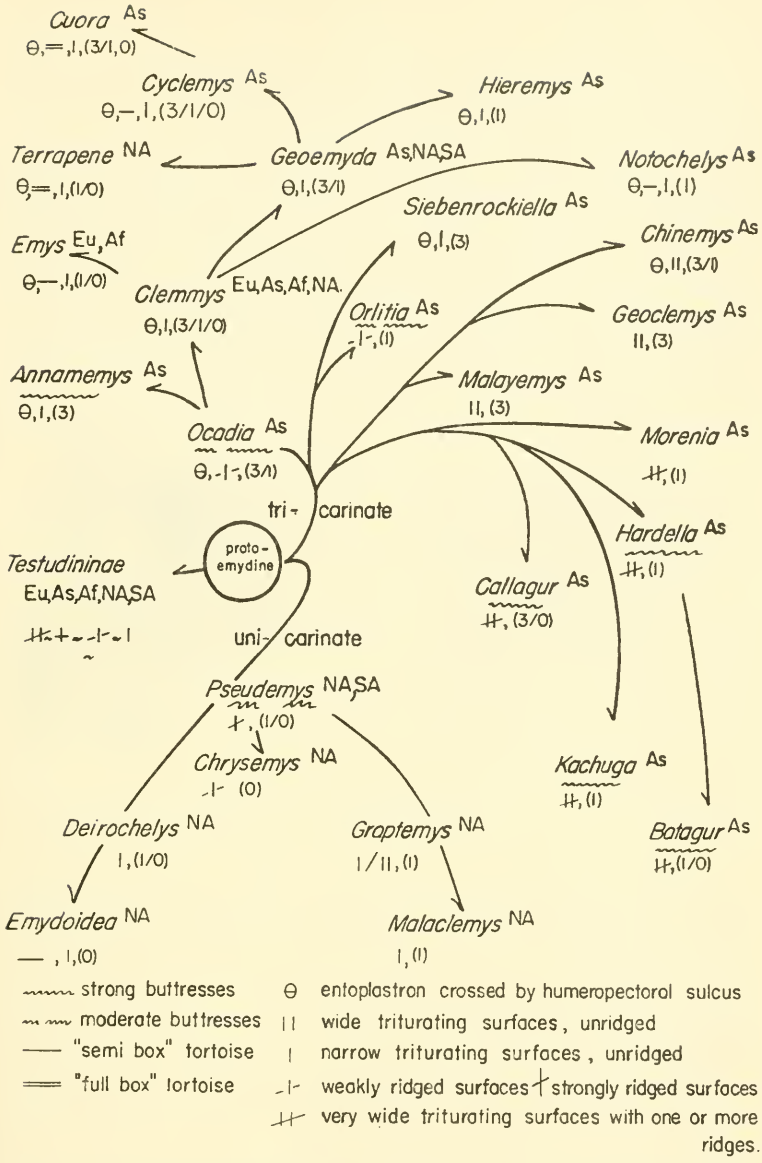


Fig. 2. Dendrogram of emydine relationships. With the exception of *Emydoidea*, the names are those of currently accepted genera. Numerals in parentheses refer to the number of keels on the carapace. NA, SA, Eu, Af, As = abbreviations for the continents on which these genera occur.

(P. Washer del.)

6. the entoplastron anterior to the humeropectoral sulcus;
7. moderate maxillary triturating ridges;
8. three keels on the rather flat shell.

The listing of these characters is somewhat in the order of our confidence in them. *Pseudemys* in the Western Hemisphere, and *Ocadia* in the Eastern, are living forms possessing most of these characters and so in our estimation closest to the postulated ancestral emydine. From the vicinity of these two central types there radiate, according to this view, three major phyletic lines, each with certain characteristic trends, and each with their subsidiary radiations.

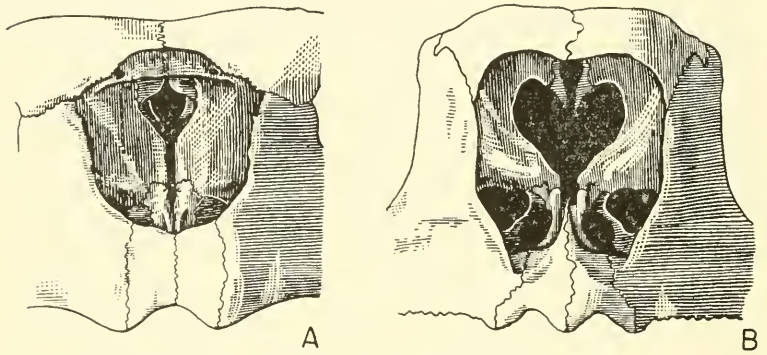


Fig. 3. Condition of the prefrontal descending process. *A*, typical emydine (*Clemmys insculpta*); *B*, typical testudinine (*Gopherus agassizii*).
(S. McDowell del.)

The land tortoises, we believe, form a unified series diverging at a very early date from the emydine stock. They appear to be united by certain parallel trends in the scalation of the head, thighs, and lower limbs; by the universal extreme weakness or absence of vertebral keeling; by the downgrowths of the frontals underarching the olfactory tract; and by a wide separation of the ventral processes of the prefrontals (in contrast to the usual median approximation of these processes in emydines, see Fig. 3). Further discussion of this lineage is given below (pp. 211-219).

Within the emydines, after the separation of the tortoise line, one major group appears to be primarily North American. This

group — *Pseudemys* and its relatives — never has a *tricarinate* carapace. One subgroup (*Chrysemys*) loses the surface sculpture of the shell and weakens the ridging of the maxillary triturating surfaces; another subgroup *Malaclemys* and *Graptemys* acquires a tuberculate condition of the median keel and a greater or lesser development of a secondary palate, while the subgroup *Deirochelys-Emydoidea* narrows the triturating surfaces, loses the maxillary ridging, elongates the head and neck, strengthens the extensor muscles of the neck with a corresponding bowing out of the carapace ribs at their point of attachment to the column and, finally, in *Emydoidea* itself achieves a plastral hinge.

The second major division of the emydines is primarily Asiatic and primitively tricarinate. This series subdivides immediately into several lines.

One lineage is that of the "river turtles" or "diving turtles" of Asia. In all, the skulls have a very characteristic habitus with a rather angular, somewhat elongate, shape and a tendency to an upturned snout; all have an extraordinarily developed secondary palate with strong maxillary ridging. Typical members of the group have extreme development of the shell buttresses, with a resulting internal partitioning of the shell far more extreme than in any other emydines — with the possible exception of *Annamemys*. Of the entire group only *Callagur* shows any trace of lateral keels on the carapace. In skull structure and general habitus *Morenia* is an obvious member of this lineage, but it has diverged radically in having the buttresses very poorly developed.

A second lineage within the major group is that of *Orlitia* and *Siebenrockiella*, a small and relatively primitive group, lacking the evident specializations of the other lines and sharing minor habitus features.

A third lineage comprises the group of Asiatic genera (united by Boulenger as "*Damonia*") which are strongly tricarinate with reduced buttresses and wide unridged triturating surfaces.

The most successful of the primarily Asiatic lineages is that to which *Ocadia* and *Clemmys* belong. This series has invaded Europe, North Africa, North America and (as *Geoemyda*) even South America.

This lineage has as its conspicuous specialization the combination of narrowing of the triturating surfaces of the skull with a bringing forward of the humeropectoral sulcus of the plastron so that it lies across the entoplastron well in front of the latter's posterior border. This series begins with *Ocadia,* a form with moderate buttressing, and proceeds in *Annamemys* to a secondary extreme development of buttresses. However, on four separate occasions (*Emys, Terrapene, Notochelys* and *Cyclemys-Cuora*) the same series has given rise to forms with hinged plastra and consequent loss of buttresses.

According to this interpretation *Emys orbicularis* is a close relative and, in fact, derivative of the genus *Clemmys,* while the species *blandingii,* here referred to the genus *Emydoidea* Gray, is considered very remote from *orbicularis* and *Clemmys,* being, instead, a close relative and derivative of the genus *Deirochelys.*

There are undoubted resemblances between *blandingii* and *orbicularis* and equally undoubted resemblances between *blandingii* and *Deirochelys reticularia.* One or the other of these sets of resemblances must be convergent.

The resemblances between *orbicularis* and *blandingii* are four in number:

1. coloration of the carapace;
2. the plastral hinge;
3. narrow maxillary triturating surfaces;
4. quadrate tending to enclose the stapes.

The last two are resemblances also to *Deirochelys.* In the face of any contradictory evidence the color character would not be regarded seriously by anyone, especially as the plastral coloration is quite different in the two species. The plastral hinge and the enclosure of the stapes are phenomena which have repeatedly occurred; the hinge has an evident adaptive value and the enclosed stapes may similarly convey some selective advantage.

The resemblance between *blandingii* and *reticularia* are generally less easy to verbalize consisting of characters in the general habitus of shell and skeleton. However, certain of these lend themselves to ready statement:

1. Both have an elongate head and neck, this elongation being more extreme than in any cryptodirous turtles except the trionychids.

2. Both have extremely narrow maxillary triturating surfaces with a very similar, gently arching, external contour.
3. Both have the orbits wholly exposed dorsally with correspondingly narrow interorbital space.
4. Both have the dorsal rib heads very slender and greatly arched, thus accommodating very powerful extensor muscles of the neck.

Dealing with these characters in the same order we offer the following comments:

1. Apparently no other emydines exhibit any tendency to elongation of head and neck, i.e., unlike plastral hinging, this is not a repeated trend.
2. This character exemplifies one of the many striking similarities in skull shape that are greater and more detailed than any to be expected except in cases of direct relationship.
3. In this orbital character it might be noted that *blandingii* and *orbicularis* are poles apart. This character also serves to separate broad groups within the Emydinae, the *Clemmys* series tending to have the orbits covered, the *Pseudemys* group tending to have them exposed dorsally.
4. The slender arched ribs are undoubtedly correlated functionally with the elongate neck, but the similarity in detail between *blandingii* and *reticularia* is far greater than between these and such a form as *Chelydra* in which powerful cervical extensors also occur.

In order to further clarify some of the modifications in our definition of *Emys*, made necessary by our new restricted concept of the genus, we append a definition of *Emydoidea*.

Genus Emydoidea Gray

1870e. *Emydoidea* Gray, Suppl. Cat. Shield Rept. Brit. Mus., part 1, p. 19. Type: *Cistuda blandingii* Holbrook (by monotypy).

1929. *Neoemys* Lindholm, Zool. Anz., 81:282 nom. nov. for *Emydoidea* Gray, considered unavailable on nomenclatorial grounds.

Definition. Beak never hooked, mesially notched; skin on hinder part of head smooth, undivided; back of thighs without tubercles; digits fully webbed.

Skull with orbits fully exposed in dorsal view; triturating surface of maxilla narrow, without ridges; anterior palatine foramina small; posterior palatine foramina large; temporal arcade complete; quadrate enclosing stapes.

Carapace smooth, never with vermiculate sculpture; neurals hexagonal, short-sided in front, broader than long; buttresses absent; rib heads slender and strongly arched to accommodate the strongly developed extensors of the long neck.

Plastron united to the carapace by ligament, a more or less distinctly developed hinge between hyo- and hypoplastra: entoplastron posteriorly touching, though usually not crossed by, the humeropectoral sulcus.

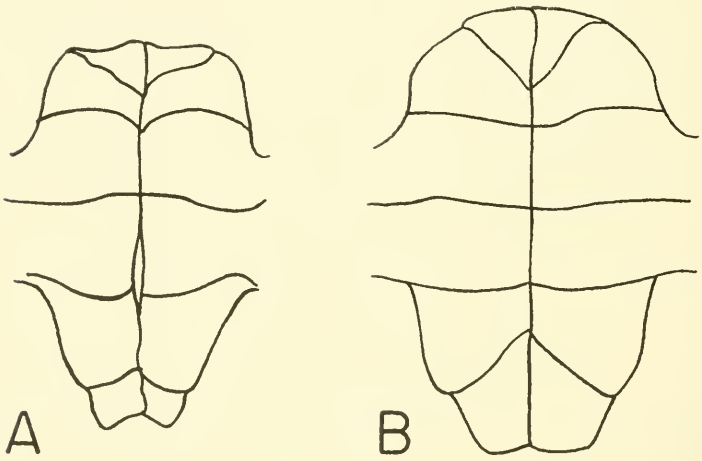


Fig. 4. Plastral shapes of juvenile African Emydinae. *A, Clemmys caspica leprosa* (M.C.Z. 53798), *B, Emys orbicularis* (M.C.Z. 1896).

(P. Washer del.)

Range. A limited area in eastern North America.

Fossil record. Known only from the Pleistocene of North America a little west of its present range.

Key to the Emydinae in Africa

Plastron never hinged; anals pointed, their median suture always shorter than the interabdominal suture (cf. Fig. 4a) . . *Clemmys caspica leprosa* (Schweigger) (p. 192)

Plastron hinged in adults; anals rounded, their median suture always longer than the interabdominal suture (cf. Fig. 4b) ..... *Emys orbicularis* (Linnaeus) (p. 202)

Genus CLEMMYS Ritgen

1828. *Clemmys* Ritgen, Nova Acta Acad. Leopold.-Carol., 14:272. Type: *Testudo punctata* Schoepff = *T. guttata* Schneider (designation by Stejneger 1907, Herpetology of Japan, p. 492).

1832. *Chelopus* Rafinesque, Atlantic Jour., 1:64. Type: *Testudo guttata* Schneider (designation by Stejneger).

1857. *Nanemys* Agassiz, Contr. Nat. Hist. U.S.,1:442. Type: *Testudo guttata* Schneider (by monotypy).

1857. *Calemys* Agassiz, Contr. Nat. Hist. U.S., 1:443. Type: *Testudo muhlenbergii* Schoepff (by monotypy).

1857. *Glyptemys* Agassiz, Contr. Nat. Hist. U.S., 1:443. Type: *Testudo insculpta* Leconte (by monotypy).

1869d. *Mauremys* Gray, Proc. Zool. Soc. London; 500. Type: *Emys fuliginosa* Gray (by original designation).

1870e. *Geoclemmys* Gray (*not Geoclemmys* Gray: 1855), Suppl. Cat. Shield Rept., part 1, p. 26. Type: *Testudo guttata* Schneider (designation by Stejneger.)

1870e. *Sacalia* Gray, Suppl. Cat. Shield Rept., part 1, p. 35. Type: *Cistuda bealei* Gray (by monotypy).

1870e. *Emmenia* Gray, Suppl. Cat. Shield Rept., part 1, p. 38. Type: *Emys grayi* Günther = *Testudo caspica* Schweigger (by monotypy).

1870e. *Eryma* Gray, Suppl. Cat. Shield Rept., part 1, p. 44. Type: *Emys laticeps* Gray = *Emys leprosa* Schweigger (by monotypy).

1919. *Melanemys* Shufeldt, Aquatic Life (Philadelphia), p. 155. Type: *Testudo guttata* Schneider (designation by Dunn, 1920. Copeia, p. 8).

Definition. Beak never hooked, not or mesially notched; skin on hinder part of head smooth, undivided; back of thighs without tubercles; digits fully webbed.

Skull with orbits largely concealed in dorsal view; triturating surface of maxilla narrow, without ridges; anterior palatine foramina small; posterior palatine foramina large; temporal arcade complete; quadrate not enclosing stapes.

Carapace smooth or with concentric grooves, never with vermiculate sculpture; neurals hexagonal, short-sided in front, as long as, or longer than, broad; buttresses short, extending only to the outer margins of the pleurals (costal bones); rib heads short, not slender or strongly arched.

Plastron united to the carapace by suture, without a hinge; entoplastron crossed by the humeropectoral sulcus well in advance of its posterior border.

Range. North America, North Africa, Europe and Asia.

Fossil record. Cenozoic of North America, Europe, Asia. The earliest occurrence in Africa is in the Pliocene of Algeria.

Key to the Forms of Clemmys caspica[1]

Plastral pattern of both young and adults predominantly dark brown or black, the bridge always dark with at most some small yellow spots or streaks. Range: South Dalmatia; Greece; Ionian Islands; Crete[1]; Cyprus; Asia Minor (only in west and south); Syria..... *c. rivulata*

Plastral pattern of both young and adults consisting of a dark brown or black blotch covering most of each shield but leaving a yellow margin, at least laterally; bridge predominantly yellow with only the sutures between the shields dark. Range: Asiatic Russia; Asia Minor (middle and east); Iraq and Iran ..... *c. caspica*

Plastral pattern *in young* consisting of a dark brown or black blotch occupying the entire medial area but leaving a wide yellow margin laterally; bridge yellow with two large dark brown blotches usually coalescing; *in adults* all markings become obsolescent. Range: Iberian Peninsula and northwest Africa (Morocco to Tunisia) south to the central Sahara, west to the Gambia (i.e. about 13°N) ..... *c. leprosa*

Clemmys caspica leprosa (Schweigger)

1812. *Emys leprosa* Schweigger, Königsberger Arch. Naturw. Math., **1**:298, 339; No locality.
1814. Schweigger, 29 (reprint of 1812).
1862b. Strauch, 18.
1894. Oliver, 101.
1896b. Oliver, 118.
1899. Doumergue, 247, pl. i.
1903. Mayet, 10.
1904. Chaignon, 2.
1907. Barbier, 73.
1919. Leblanc, 177.
1824. *Emys marmorea* Spix, Animalia nova Species testud. ranarum Brasil . . ., p. 13, pl. x; No locality.
1831c. Gray, 25.

1 We are without material of *C. c. cretica* Mertens (1946, Senckenbergiana, **27**: 115) of Crete, which appears to differ but slightly from *c. rivulata*.

1835. Duméril and Bibron, 248.
1829. *Clemmys Sigriz* Michahelles, Isis von Oken, col. 1295; Spain.
1831. *Terrapene sigriz* Bonaparte, 87 (translation of last).
1831c. *Emys vulgaris* Gray, Synopsis Reptilium, p. 24, pl. iv: Southern Europe.
1831b. Gray, 9 (Spain).
1841. Schlegel, 108.
1860. Tristram, 405 (Sahara).
1833. *Les Emydes* Rozet, 231.
1835. *Emys sigriz* Duméril and Bibron, 240.
1850. Guichenot, 2.
1854. Eichwald, 415.
1887. Lortet, 19, pl. vii.
1897. Bateman, 54.
1836. *Emys lutaria* Bell (part: not of Lacépéde), text and col. pls.
1844. *Emys caspica* Gray (part: not of Gmelin), 19.
1855. Gray, 22.
1867a. Steindachner, 5.
1854. *Emys laticeps* Gray, Proc. Zool. Soc. London, 1852, p. 134: Gambia River, West Africa (M. Castang coll.).
1855. Gray, 23, pl. ix.
1857. *Tortue aquatique* Labouysse, 83.
1860c. *Emys fuliginosus* Gray, Proc. Zool. Soc. London, p. 232, pl. xxx: North Africa?
1862a. *Clemmys laticeps* Strauch, 32.
1865. Strauch, 75.
1884a. Rochebrune, 18.
1862a. *Clemmys marmorea* Strauch, 32.
1865. Strauch, 75.
1862a. *Clemmys leprosa* Strauch, 122.
1865. Strauch, 74.
1880c. Vaillant, 33, 88.
1889a. Boulenger, 105.
1889b. Boulenger, 306.
1890. Strauch, 69.
1891c. Boulenger, 96, 106.
1892. Anderson, 11.
1892. König, 15.
1894. Werner, 76.
1895. König, 404.
1896. Escherich, 278.
1898. Jeude, 7. (*Clemnys*)
1900. Boettger and Tornier, 64.
1901. Gadow, 357, fig. 80 (skull).

1908. Kerville, 96.
1908. Zulueta, 451.
1909. Siebenrock, 481.
1911. Lampe, 144.
1912. Kollman, 101, figs. 1, 3, 4. (*Clemnys*)
1912b. Pellegrin, 262.
1912b. Werner, 408.
1913. Pellegrin (1912), 420.
1914. Pellegrin, 347.
1914b. Werner, 334.
1916e. Chabanaud, 233.
1917c. Chabanaud, 105.
1918. Seurat, 23.
1920. Mourgue, 233.
1925. Flower, 922.
1926a. Pellegrin (1925), 315.
1926e. Pellegrin, 121.
1927. Fejérváry, 517.
1927a. Pellegrin, 261.
1929. Dollfus, 112.
1929. Flower, 17.
1929b. Werner, 12, 15, 21.
1930. Seurat, 182.
1931c. Werner, 275.
1932. Ghigi, 208.
1934. Mosauer, 51.
1935. Laurent, P., 345.
1935. Hediger, 3.
1937. Hediger, 187, 191.
1938. Angel and Lhote, 376.
1938. Gorham and Ivy, 181.
1947. Braestrup, 5.
1950c. Villiers, 343.
1950. Williams, 550.
1951. Aellen, 168, 195.
1952. Stemmler-Morath, 217, photos 1-2.
1953c. Girons, 76, 79.
1954. Noël-Hume, 90, 112.
1865. *Clemmys fuliginosa* Strauch, 76.
1869d. *Mauremys laniaria* Gray, Proc. Zool. Soc. London, p. 499, pl. **xxxvii**: No locality (ex Zool. Gardens from a dealer).
1869d. *Mauremys fuliginosa* Gray, 500.
1870e. Gray, 35.
1872. Sclater, P. L., 603 (synonymizes with *leprosa*).

1873b. Gray, 35.
1869c. *Emys flavipes* Gray, Proc. Zool. Soc. London, p. 643; No locality.
1869c. *Emys fraseri* Gray, Proc. Zool. Soc. London, p. 643: North Africa (ex Mr. Fraser).
1870e. Gray, 36.
1873b. Gray, 35.
1873d. Gray, 146.
1870e. *Emys laniaria* Gray, 37.
1870e. *Eryma laticeps* Gray, 45.
1873b. Gray, 36.
1873b. *Emys lamaria* (*sic*) Gray, 36.
1874. *Emys caspia* var. *leprosa* Boettger, 126.
1882. *Clemmys caspica sigriz* Bedriaga (1881), 340.
1883a. *Clemmys caspia* var. *leprosa* Boettger, 131.
1886. *Clemmys Caspica* Parenti and Picaglia (not of Gmelin), 86.
1927. *Clemmyde lépreuse* Seurat, 81.

Synonymy. Schweigger (1812) cites Schoepff as the author, having taken the name from an unpublished manuscript of the latter. He had seen the type in the Paris Museum.

Common Names. Leprous Terrapin (preferred); Marbled Terrapin (Gray: 1831c); Mud Tortoise (Tristram: 1860); Iberian Water-Tortoise (Gadow: 1901); Spanish Terrapin (Flower: 1929); *Fakroun-el-ma* (Arabic: Doumergue: 1899).

Illustrations. This terrapin is well represented in the fine colored plate of Lortet (1887: pl. vii).

Description. Beak distinctly notched; edge of jaws not or but finely denticulated; mandibular width at symphysis less than (young) or almost equal to (adults) the horizontal diameter of the orbit; skin on upper surface of head undivided; forelimb anteriorly covered with smooth, flattened shields of very diverse size of which about 5 (3 along outer margin and usually 2 internal to them) greatly enlarged; digits webbed to the 5 claws; hind foot strongly webbed, claws 4; tail long.

Carapace rather strongly depressed, anterior and posterior margins not expanded, not or but feebly reverted, not serrated, not notched — at most but slightly incurved — in nuchal region; nuchal moderate, *broader than long,*[1] wider posteriorly; vertebral keel distinct in young[2] but scarcely distinguishable in some

1 Longitudinally divided in an Algerian terrapin (Strauch: 1890).

2 Up to individuals of about 120 or 130 mm. according to Doumergue (1899: 51) who has additional notes on growth changes.

adults; vertebrals 5, rarely 6,[1] broader than long, broader than the costals (young) or variable (adults); costals 4, costal (lateral) keels present but interrupted and indistinct; marginals (exclusive of nuchal and supracaudals) 11; supracaudal divided.

Front lobe of plastron anteriorly truncate, not or but slightly produced, not notched, slightly concave in ♂ ♂, flat or convex in ♀ ♀; gulars paired; pectorals wide; axillary 1, moderate; inguinal 1, moderate, not in contact with femoral; hind lobe broadly or deeply notched, anals pointed (cf. Fig. 4 for contrast with *Emys*).

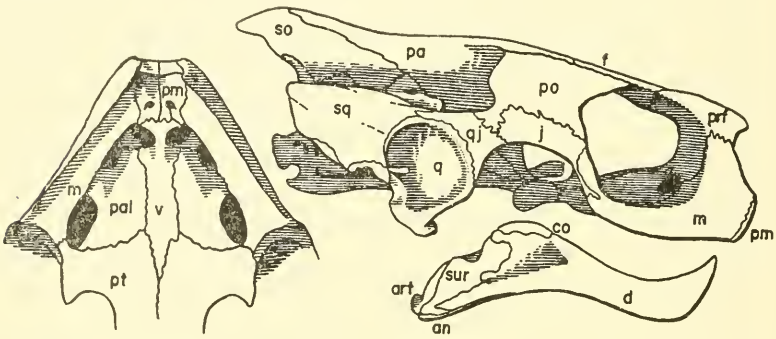


Fig. 5. Skull of *Clemmys caspica leprosa* (M.C.Z. 2210). Condylobasal length 39 mm. *an* = angular; *art* = articular; *co* = coronoid; *d* = dentary; *f* = frontal; *j* = jugal; *m* = maxillary; *pa* = parietal; *pal* = palatine; *pm* = premaxillary; *po* = postorbital; *prf* = prefrontal; *pt* = pterygoid; *q* = quadrate; *qj* = quadratojugal; *so* = supraoccipital; *sq* = squamosal; *sur* = surangular; *v* = vomer.

(S. McDowell del.)

Plastral formula: Abd > or = (p > or = or < f) > (an > or = or < g) > h.

Color. Carapace of young pale or dark olive to olive brown, uniform, or each costal shield with a black-bordered yellowish spot or streak; the vertebrals with a narrow or broad median streak; marginals uniform or each marbled with yellow to a variable degree, frequently edged with yellow laterally. When any pattern is present each shield is apt to be narrowly edged with black, becoming more or less uniform in adults.

[1] Six in a specimen from Aïn Sefra (M.C.Z. 27345).

Plastron of young yellow with the central area dark brown (with or without a median light line), and dark brown blotches usually coalescing on the bridge; marginals ventrally exhibit dark brown blotches at the sutures. Both plastron and marginals more or less uniform without definite pattern in adults.

Head olive to olive gray, its sides streaked or vermiculated with yellow (reddish orange), between eye and tympanum a small round yellow (orange) spot usually present, around the tympanum a more or less well-defined ring of yellow (orange); sides of neck olive gray with 4 or 5 longitudinal yellow (orange) streaks; throat streaked or vermiculated with yellow (orange); limbs olive streaked or vermiculated with yellow (orange).

In life, judging by the detailed description given by Bedriaga (1882), the coloration would appear to be even more striking than suggested by our description. However, according to Mosauer (1934), considerable color variation occurs between juveniles from different localities such as Gabes and Gafsa. In old individuals all bright markings tend to disappear. For further color changes due to age, see Doumergue (1899: 52).

Breeding. Mating takes place either on land or in water, usually on the surface though sometimes a mated pair will descend to the bottom where they may remain immobile for several hours (Lortet: 1887). The artificial conditions of captivity that render hibernation unnecessary, upset the breeding behavior so that eventually mating may take place at any time of the year. In his eagerness to secure a mate the ♂ is apt to bite at the collarlike folds of skin within which the ♀ withdraws her head. His repeated attentions result in sores and swellings that in due course prevent the ♀ from wiping her eyes with the back of a forefoot — a practice common to many species. Ultimately the eyes fester and the terrapin becomes almost blind, gives up feeding, and leaves the water in a condition that is very difficult to cure (Gadow: 1901).

Early May, according to Lortet (1887) is the usual month for laying. Doumergue (1899), however, records that between the evening of September 2 and the following morning a large Algerian ♀ laid 9 white eggs ranging in size from 21 x 34.5 to 21 x 38 mm. Usually 6 to 8 are deposited in shallow excavations in mud, sand, or between the roots of a tree. Twenty-five

days after the eggs have been laid, hatching takes place (Lortet: 1887). In Tunisian oases, towards the end of May, hatched-out eggshells were encountered in small holes, chiefly between the roots of trees, bordering the waterholes. No hatchlings were seen, however (Mosauer: 1934).

Upon hatching, the young immediately hasten to the water where few remain near the surface or venture to bask on the rocks; instead they dive to the bottom where they hide in the mud. There, by means of a net, large numbers can be captured with comparative ease (Lortet: 1887). The carapaces of many young measured on April 13, 1898, were 30 mm.; by mid-August they had increased to 45 mm. (Doumergue: 1899).

Longevity. Despite their dispensing with seasonal rest as a result of congenial climatic conditions, most of Gadow's many captives lived "with undiminished appetites for more than twelve years" (Gadow: 1901). A terrapin in the Giza Zoological Gardens lived for 5 years, 1 month, and 10 days; another in the London Zoo only survived 4 years, 6 months, twelve days (Flower: 1925b).

Diet. Hatchling terrapins are eaten by old ones (Doumergue), though the principal food of this species consists of frogs, toads, tadpoles, fishworms, aquatic insects and their larvae (Lortet). Twenty terrapins were observed feeding on the corpses of horses that had fallen into the water (Rozet: 1833). In the absence of animal food these essentially carnivorous reptiles will eat algae and aquatic plants (Labouysse: 1857), lettuce, legumes and scraps of bread (Doumergue). By seizing bait and getting hooked they constitute a nuisance to fishermen (Labouysse).

Clearly Lortet errs when he says that the prey is always devoured under water, for Stemmler-Morath (1952) often found some feeding on Arab excrement on the far side of an earthen wall at least a yard from the nearest water. Another half-dozen were found in a dry ditch used by natives as a toilet. They were in good health and were said to have lived there as long as a local farmer could remember.

Parasites. The name *leprosa* refers to the leprous appearance of the carapace resulting from attacks by freshwater algae, to which this terrapin is especially prone owing to its manner of life. When the mud-encrusted reptile emerges from its slimy

pool to bask in the hot sun, its horny shields tend to become brittle and flake off. Entering through the cracks, the algae flourish in the Malpighian layer and even in the underlying bone, which becomes gangrenous in places. Terrapin inhabiting permanent lakes or watercourses are not subject to attack and remain as clean as other species (Gadow: 1901). Stemmler-Morath (1952) remarks that these green and brown algae may attain a length of as much as 50 mm., and were present on all the specimens caught by him. Seurat (1918) has recorded three species of nematodes (*Camallanus microcephalus; Falcaustra lambdiensis,* and *Spiroxys contortus*) from Algerian terrapin.

Enemies. Hundreds were on sale in the fish market at Algiers (Strauch: 1865). As previously mentioned, small terrapin are eaten by the adults (Doumergue: 1899). At Rabat one terrapin was recovered from the stomach of a heron (Pellegrin: 1926a).

Defense. Apart from seeking safety by burying themselves in the muddy bottom of their habitat, the chief defense of these terrapin would seem to be their odoriferousness. This derives from a large pair of inguinal glands that open just behind the plastral bridge. Freshly caught *leprosa* emit a powerful stench, but captive specimens cease to do so after becoming accustomed to being handled (Gadow: 1901).

Apparently the odor may be influenced by diet, for at times it reeks of fish and an excess of animal food increases its intensity (Werner: 1912b). Doumergue (1899) claims that the smell is scarcely noticeable in winter and early spring, but we reject his deduction that the odoriferousness of these terrapins derives from the mud in which they live, and tends to disappear when they are kept in clear water.

Temperament. Excessively wary, scrambling into the water when anyone approaches to within ten or five meters. Such behavior makes their capture difficult. Why they should be so nervous is not readily explained, for Moroccans do not molest them and no other potential enemy is in evidence (Stemmler-Morath: 1952). This opinion is certainly inapplicable to Algerian Arabs if Strauch's statement (1865) holds good today (cf. *Enemies*).

Aestivation and Hibernation. During the hot summer months (August-September), as ponds and watercourses shrink in the

torrid heat, these terrapin crowd into the remaining pools. There their numbers contribute to the daily increasing foulness of the stagnant water until everything edible is consumed. Then the reptiles leave the pool to seek shelter among the rocks where they bury themselves until aroused by the return of rainy weather.

During the winter months (November-March) hibernation occurs but is intermittent (Lortet: Doumergue: Aellen). These terrapin neither aestivate nor hibernate in captivity when temperature conditions are congenial and a current of warm water is kept circulating through their tanks. However, Gadow's terrapins showed a fondness for the hot-water pipes against which dozens of them would huddle until their shields, and even the plastral bones, suffered from the excessive heat. To prevent recurrence of such injuries it was found necessary to keep the reptiles away from the pipes by screening. Some *leprosa* in an English garden successfully passed the winter under a heap of moss and rubbish; others remained in the mud beneath the ice in a deep concrete pond where they survived several very severe winters to emerge each spring in perfect health (Gadow: 1901).

Habitat. Many early travellers — from Rozet (1833) onwards — record the astonishing abundance of *leprosa* in Algeria, where scarcely a pool, stream or river is without some terrapins. Werner (1894), however, considered it less common in east Algeria than in the west. In Morocco they are present in almost incredible numbers in all bodies of water except the most temporary of desert streams (Stemmler-Morath: 1952). The latter writer found terrapins living in the swift streams of the High Atlas, an observation that appears to qualify Werner's statement that *leprosa* prefers level country. He also found half-a-dozen individuals living in a ditch some distance from water, as is recorded under *Diet.*

Localities. Spanish Morocco: *Larache (U.S.N.M.); Tangier (Tanger). *French Morocco:* Aïn el Auda; Behalil near Sefrou; Berguent; Bin el Ouidan (Ouidane); Casablanca; Daïet el Roumi; Fes (Fez); Mogador; *Oudjda; Oued Akrech (Akreuch), south of Rabat; Oued Berkine; Oued Fes; Oued Ifrane, middle Atlas; Oued Imoughoud (Tmoughout), south of Taza; Oued Ksib near Mogador; Oued Liboud; Oued Sebou; Oued Sous; Oued Tensift; Oued Tiflet; Oued Yguem (Yquem); Oued Za; Ouezzane; Rabat;

Sehoul; *Sidi Yahia; Sous; Taourirt; Tetouan (Tetuan). *Algeria:* Aïn el Bahir; Aïn el Hadjar; Aïn Sefra; Aïn Temouchent; *Algiers (Alger); Arba; Arlal; Aumale; Batna; Bedeau; *Biskra (U.S.N.M.); Biskra to Constantine; *Bone; Bordja Saada; Boudsareah; *Bou Saada; Cheliff (Chelif); Constantine; Der Kaid Embarek (Embareek M'Toughi); El Khreider; Geryville; Hamman Salahine near Biskra; Lake Fetzara (Tetzara; Tetzura); Maeta; Medea; Oran; Ouargla; Oued Andalouses at Bredeah; Oued Asseila (? Asselar); Oued Baccaura; Oued el Biodh; Oued el Harrach; Oued Safsaf at Tlemeen; Oued Saida at Aïn el Hadjar; Oued Sebaou near Tizi Ouzou; Oued Sig (Zig); Oued Tafna at Sebdou; Oued Tlelat; Perregaux; Rhadames; Sahara; Touggourt; Ziban Oases. *Tunisia:* Aïn Draham; Aïn Hameraia; Bir Meherga to Zaghouan; Djerba Id.; Douirat (Duirat); El Hamma (Hamman) near Tozeur; Gabes; Gafsa; Ischkeul; Kairouan (Kairwan); Maxula Rades; Oued Bagra; Oued Debbane; Oued el Amor; Oued el Mahdi; Oued Gued-ouiaris; Oued Leben; Oued Miliani (Milane); Oued Oum Mela; Oued Rzella; Oued Siliana; Soliman; Tabarca; Tozeur (Touzla; Tozzer); Zaghouan. *Libya:* Murzuch (Murzouk) in Fezzan; Tripolitania. *French West Africa:* Adrar des Iforas; Agades (Agadez), Aïr region; Fort Gouraud or Idjil (probably Koudja d'Idjil), Mauretania. *Gambia:* Gambia River (Gray: 1853).

Range. Iberian Peninsula and north Africa (Morocco to Libya) south to the central Sahara, west to the Gambia (i.e. about 13°N.). We reject the record of Porto Novo, Dahomey (Chabanaud: 1917c).[1]

Genus EMYS Duméril

1806. *Emys* Duméril (part), Zool. analytique, p. 76. Type: *Testudo lutaria* Linnaeus = *T. orbicularis* Linnaeus (designation by Fitzinger, 1843, Syst. Rept., Part 1, p. 29).

1814. *Hydrone* Rafinesque, Specchio Sci. (Palermo), 2, p. 66. Type: *T. orbicularis* Linnaeus (by present designation).[2]

1844. *Lutremys* Gray, Cat. Tortoises, Crocodiles, Amphisbaenians in Brit. Mus., p. 31. Type: *Testudo europaea* Schneider (by monotypy).

1 This record should be discarded. Dr. Chabanaud (1917c:105) who identified the two specimens, informs us (22.xii.55) that they were subsequently destroyed with other material identified at that time. Furthermore nothing concerning the itinerary of the donor (Waterlot) can be found in the Museum records at Paris.

2 The included species were *T. orbicularis, lutaria* and *geometrica.*

Definition. Beak never hooked, mesially notched; skin on hinder part of head smooth, undivided; back of thighs without tubercles; digits fully webbed.

Skull with orbits wholly concealed in dorsal view; triturating surface of maxilla narrow, without ridges; anterior palatine foramina small; posterior palatine foramina large; temporal arcade complete; quadrate barely enclosing stapes.

Carapace smooth or with concentric grooves, never with vermiculate sculpture; neurals hexagonal, short-sided in front, as long or longer than broad; buttresses absent; rib heads stout, not slender or strongly arched.

Plastron united to the carapace by ligament, a more or less distinctly developed hinge between hyo- and hypoplastra; entoplastron crossed by the humeropectoral sulcus well in advance of its posterior border.

Range. North Africa, Europe and contiguous parts of Asia.

Fossil record. Most fossil species assigned to this genus do not really belong to it. Perhaps the only certain records are those from the Pleistocene of Europe.

Emys orbicularis (Linnaeus)[1]

1758. *Testudo orbicularis* Linnaeus, Syst. Nat., ed. 10, **1**, p. 198: Southern Europe.

1766. Linnaeus, 351.

1758. *Testudo lutaria* Linnaeus (part), Syst. Nat., ed. 10, **1**, p. 198: "Italia, Oriente."

1783. *Testudo Europaea* Schneider, Naturg. Schildkröten, p. 323: most countries in Europe.

1819. Bojanus, 1-178, figs. 1-201 (anatomy).

1788. *La Jaune* Lacépède, Hist. Nat. Quad. Ovip. Serpens, **1**, p. 135, and *Testudo flava* at end of same volume in Synopsis methodica, a table in which binomials are employed: Europe (other localities in error).

1790. *Testudo meleagris* Shaw, Nat. Misc., **4**, pl. cxliv: "America" (in error).

1792. *Testudo pulchella* Schoepff, Naturg. Schildkröten, p. 134, pl. xxvi (ed. 2, 1801, p. 113, col. pl. xxvi): No locality.

[1] In conformity with our practice we have included all known synonyms; in this instance, however, our *orbicularis* material is too inadequate for us to express an opinion as to whether any of them are possibly recognizable geographical races. We have omitted "*Emys antiquorum* Valenciennes," listed as a synonym by Gray (1855:41) as no such name was found in the reference he gives.

1802. *Testudo rotunda* Sonnini and Latreille, Hist. Nat. Rept., **1**, p. 107; **2**, p. 282: No locality (Sometimes attributed to Lacépède (1788) who, however, uses only the French equivalent in conjunction with *orbicularis*).

1833. *Cistuda hellenica* Bibron and Bory de Saint Vincent, Reptiles et Poissons, *in* Bory de Saint Vincent Exped. Sci. Morée, **3**: Zool. 1, p. 61: Nisi Plain, Pamisus Basin, Messina, Greece.

1833. *Emys hellenica* Valenciennes (for plate only) *in* Bory, *op. cit.*, Atlas, pl. viii, figs. 2-2a.

1833. *Emys iberica* Valenciennes (for plate only) *in* Bory, p. 61, *op. cit.*, Atlas, pl. ix, fig. 1.

1836. *Emys Hofmanni* Fitzinger, Ann. Wiener Mus., **1**, p. 123: *n.n.* to combine *hellenica* with *orbicularis*.

1850. *Cistudo Europaea* Guichenot, 2.

1860. Tristram, 405 ("Sahara" applied erroneously).

1899. Doumergue, 252.

1904. Chaignon, 3.

1925a. Seurat, 150.

1851. *Emys lutaria* Bianconi, 71.

1862a. Strauch (part), 101.

1865. Strauch, 49.

1897. Bateman, 50, fig. 34 (habits in captivity).

1854. *Emys europaea* Eichwald, 416.

1877. Bruhl, pl. xxxiii, figs. 8, 14; pl. xxxiv, figs. 4, 9.

1880. Bruhl, pl. lxix, figs. 3-4.

1915. Rawitz, 671, pl. xlix, figs. 76-78.

1855. *Lutremys europaea* Gray, **1**, 40 (*Lutremys* was proposed in 1844).

1887. Lortet, 15, pl. vi (did not encounter any when in Africa).

1862b. *Cistudo lutaria* Strauch, 17.

1867. Lallement (not seen).

1894. Oliver, 101.

1889a. *Emys orbicularis* Boulenger, 112.

1891c. Boulenger, 96, 105.

1896. Doumergue, 477.

1897. Siebenrock, 247, pl. iii, fig. 14.

1901. Gadow, 351, fig. 79.

1907. Johnson, 13, 69, photo.

1908. Kerville, 96.

1909a. Siebenrock, 486.

1912b. Werner, 412, fig. (not used).

1913. Pellegrin (1912), 420.

1920. Mourgue, 233.

1925b. Flower, 922.
1927a. Pellegrin, 261.
1929. Dollfus, 112.
1930. Seurat, 179.
1937a. Flower, 4.
1938. Gorham and Ivy, 181.
1951. Aellen, 169, 195.
1954. Noël-Hume, 94, 112.

1903. *Emys orbicularis hellenica* Kovatscheff, Verh. Zool.-Bot. Ges. Wien, **53**, 171 (revives name as subsp.).

1916. *Emys orbicularis aralensis* Nikolsky, Faune Russie, Rept., **1**, p. 24: Lake Aral (presumably Aral Sor, just north of the Caspian Sea, Astrakhan, U.S.S.R.).

1934a. *Emys orbicularis orbicularis* Mertens and Müller *in* Rust, 7.

Another citation of *Emys lutaria* will be found under *Clemmys caspica leprosa*. An extensive bibliography of *orbicularis* is furnished by Boulenger (1889a), and another by Siebenrock (1909). After careful checking we have omitted most of them from the above list as they deal exclusively with European or Asiatic material; a selected few have been included on account of their taxonomic importance or because of the observations that they contain.

Names. European Terrapin (preferred); European Pond Tortoise (Flower: 1929); Speckled Terrapin (Shaw: 1790); Mud Tortoise (Bateman: 1897).

Illustrations. This terrapin has often been well figured, though usually from European specimens as in the colored plate of Lortet (1887:pl. vi).

Description. Beak distinctly notched; edge of jaws smooth; mandibular width at symphysis less than (young) or subequal to (adults) the horizontal diameter of the orbit; skin on upper surface of head undivided; forelimb anteriorly covered with smooth, flattened shields of very diverse size, of which none is conspicuously enlarged; digits webbed to the 5 claws; hind foot strongly webbed, claws 4; tail long.[1]

Carapace moderately depressed, anterior and posterior margins not expanded, not reverted, not serrated, not notched in nuchal region; nuchal moderate to small, longer than broad; dorsal shields concentrically striated except in aged specimens; verte-

[1] Alleged age and sexual distinctions displayed by tail length that are mentioned by Boulenger (1889a:113) are not discernible even in our limited material.

bral keel distinct in young but scarcely distinguishable in adults; vertebrals 5, broader than long, broader than the costals (young) or narrower than the costals (adults); costals 4, with indistinct, interrupted keels (young) or without trace of keels (adults); marginals (exclusive of nuchal and supracaudals) 11; supracaudal divided.

Front lobe of plastron anteriorly truncate, not produced, not notched, possibly slightly concave in ♂ ♂, flat or convex in ♀ ♀, hinged at humeropectoral suture; gulars paired, rarely two pairs;[1] pectorals wide; axillary 1,[2] moderate; inguinals variable, often indistinct, not in contact with femoral; hind lobe very broadly or not notched; anals truncate or rounded, not pointed (cf. Fig. 4, for contrast with *Clemmys*).

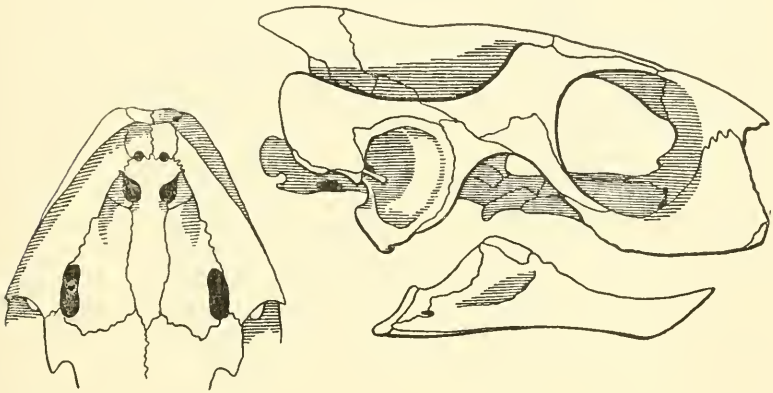


Fig. 6. Skull of *Emys orbicularis* (A.M.N.H. 73604). Halfgrown. Condylobasal length 28 mm. Certain features of this specimen are due to its comparative youth. (S. McDowell del.)

Plastral formula: An > (g, p, abd subequal) > f > h.

Color. Carapace of young, dark brown or black, uniform, or with more or less numerous yellowish dots or radiating lines. Adults similar.

Plastron of young, dark brown or black, the outer side of each plastral shield and underside of each marginal with a large

[1] Two pairs in an Algerian specimen (U.S.N.M. 10986).

[2] Occasionally 2, as on right side of a Tiflis terrapin (M.C.Z. 5309).

yellow spot. Plastron of adult nearly entirely blackish brown, brown and yellow, or yellow, each shield more or less narrowly edged with black. Adults similar.

Head above, dark brown or black, uniform, or spotted or vermiculated with yellow; sides of head and throat spotted or ver-

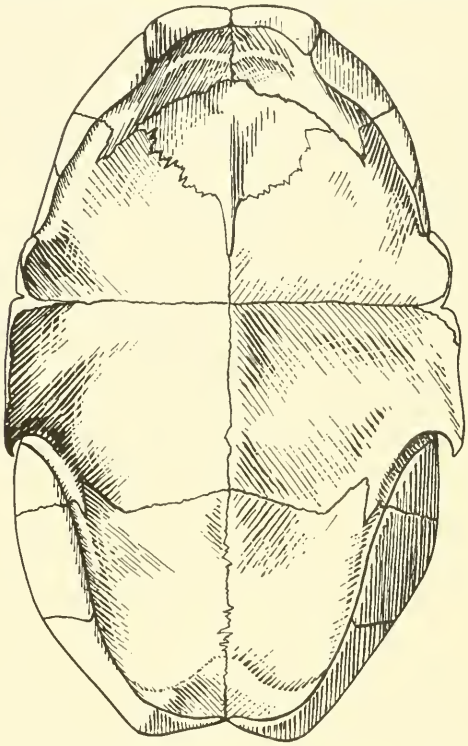


Fig. 7. *Emys orbicularis* (M.C.Z. 31976) Internal view of plastron. x 2/3. (P. Washer del.)

miculated with yellow, the latter sometimes predominating on the throat; limbs and tail dark brown or blackish, more or less sparsely spotted with yellow, the tail streaked with yellow.

We are unable to confirm Boulenger's statement (1889a) that the color of the spots has a sexual significance, i.e. yellow in ♀, pale brown in ♂. Gadow (1901) states that both the color and

shape of the carapace alter with age.

Size. Carapace length of largest ♂ (M.C.Z. 5187) from Algiers, 128 mm., breadth 94 mm., height 48 mm.; carapace length of largest ♀ (M.C.Z. 5189) from Algiers, 138 mm., breadth 96 mm., height 62 mm. Both far surpassed by an unsexed European record of 190 mm. (Boulenger: 1889a). A juvenile (M.C.Z. 3482) from southern Europe has a carapace length of 30 mm., breadth 24 mm., height 14 mm.

Sexual dimorphism. Both tail length and spotting were believed by Boulenger (1889a) to be indications of sex, but we have been unable to confirm his findings with the limited material at our disposal.

Breeding. On warm spring nights during the pairing season these terrapins emit short piping calls until they find a mate, after which the couple swim about together.

When gravid, the ♀, having selected a suitable spot free of vegetation, where the soil is firm, prepares the site by ejaculations of fluid from the bladder and anal water-sacs. Then, holding her body rigid while stiffening the tail, she uses the latter as a borer, pushing it into the ground. Following this preparatory loosening of the soil, it is scooped out and heaped around the periphery of a hole that may be as much as five inches in depth, i.e. as far down as her hind feet can reach. The feet are also employed to separate and spread the eggs which are deposited in a single layer on the bottom of the pit.

After about 10 eggs have been laid, the loose soil is returned to the hole and tamped down by allowing the plastron to fall upon it as, time and again, the terrapin raises herself to her full height and then drops on the site. After some additional stamping over the area, the terrapin roughens the surface with her claws before leaving the place for good.

The incubation period varies in relation to locality and temperature, embryos sometimes hibernating within the egg. In a garden at Kiev, U.S.S.R., some eggs did not hatch until 11 months after they were laid. For some obscure reason, hatchlings of *orbicularis* are more difficult to rear than are those of other terrapin. (The foregoing remarks probably refer to European specimens and are taken from Gadow: 1901.)

Growth. One hatchling, reared in captivity, which wintered beneath moss in an unheated room in England, took 4 years to

attain a carapace length of 50 mm. A 25 mm. terrapin grew to 134 mm. in carapace length during 11 years, at the end of which time it weighed 491 grams (about 1 lb.). Another, over a period of 8 years, increased in carapace length from 110 to 132 mm., and from 83 to 106 mm. in breadth. This particular terrapin, however, did not hibernate as it was kept in a greenhouse (Gadow: 1901).

Longevity. Perhaps the best authenticated record is 27 years, 11 months, 17 days, in the Jardin des Plantes (Vaillant:1892:223[1]) cited by Flower (1925b) who, however, (1937a) refers also to a ♀, already adult in 1868, which bred regularly for 60 years in a French garden until her death on February 27, 1928. This, and a record of 120 years, are taken from Rollinat (1934:110[2]). Probably all these instances of longevity are based on French, rather than African, terrapins.

Diet. In captivity young European Terrapins will readily take flies, tiny worms or tadpoles; larger individuals eat insects, frogs, fish and even raw meat. Though normally feeding in water, tame terrapins will come out on land to be fed if sufficiently hungry. Usually, however, the prey must be seen in motion before a terrapin will attack it.

Frogs are stalked as they sit on a floating leaf. Rising slowly from below, the terrapin thrusts its nostrils and eyes above the surface close to the frog and waits motionless. After a while it may sink to rise again with its snout actually touching the unsuspecting frog's toes which, after smelling at them, it seizes with a sudden sidewise biting motion. While maintaining its hold the terrapin employs its sharp foreclaws to tear the living prey to pieces. This occupies considerable time for only the intestines and scraped-off flesh are devoured.

Fish too are stalked, the terrapin moving slowly along the bottom as it cautiously approaches its prey. Then, with a few gentle movements of its fully-extended webbed feet, the reptile rises almost imperceptibly and, gaping widely, grabs at the fish's belly. The bones are picked clean as the skeleton sinks to the bottom, but the air-bladder floats away on the surface to serve as an indication of the presence of a terrapin in the pond (Gadow:1901).

1 Vaillant, L., 1892, Arch. Mus. Paris (3), 4, pp. 221-253.
2 Rollinat, R., 1934, La Vie des Reptiles de la France Central (Paris).

Defense. The European Terrapin lacks a defensive odor like that which is so characteristic of *Clemmys* (Gadow:1901).

Hibernation. In Europe this terrapin buries itself in mud and does not reappear until spring is well advanced (Gadow:1901).

Migration. At times, extended migrations take place, either under the stimulus of a food shortage or because the occupied pool is in process of drying up (Gadow:1901).

Habits. European Terrapins should not be kept in an aquarium unless there is growing vegetation and facilities to land, stones to bask on and bark or moss under which they can retire when so inclined (Bateman: 1897; Gadow:1901).

Habitat. The statement as to the abundance of this terrapin in Algeria, made by Guichenot (1850), is due to confusion with *Clemmys,* according to Boulenger (1891c). The same author points out that its reported occurrence in the "Sahara" by Tristram (1860) is due to a misapplication of this term to the high plateau of southern Algeria. The frequency with which *Emys* occurs in Tunisian streams in the absence of *Clemmys,* or *vice versa,* is remarked upon by Chaignon (1904); however, both apparently coexist in a dozen localities.

Localities. French Morocco: Oued Ifrane; Oued Nkhol. *Algeria:* *Algiers; Bone; La Calle; Lake Fetzara; Oued Harrach; Oued Sebaou (as Wed Sebaou); "Sahara" (in error). *Tunisia:* Aïn Draham; Cap Bon streams; Krombalea to Soliman; Oued Belli; Oued Bezirk; Oued el Amor; Oued el Kebir; Oued Melah (as Mala); Oued Sidi Saad, 3 km. south of Cebala; Tabarca (as Taborca).

Range. Northwest Africa (Morocco to Tunisia); central and south Europe; southwestern Asia.

Formerly the range was much more extensive. Post-glacial remains have been found in Sweden, Denmark, the Netherlands and in the peat of England (Norfolk and Cambridgeshire). According to Bateman (1897) specimens that have escaped from captivity survive English winters, having been recaptured in a healthy condition years later.

Subfamily TESTUDININAE

1909. *Testudininae* Siebenrock, Zool. Jahrb. Syst., Suppl., 10, p. 508.

Definition. Testudinid tortoises of strictly terrestrial habit. Skin of head divided into larger or smaller shields; scales on

forelimb more or less enlarged, often with dermal ossifications; hinder side of thigh often with large spurlike tubercles: scent glands absent; bursae anales absent.

Skull with prefrontals whose descending processes are more or less widely separated inferiorly; frontal entering or excluded from orbit; postorbital tending to be reduced, rarely absent;

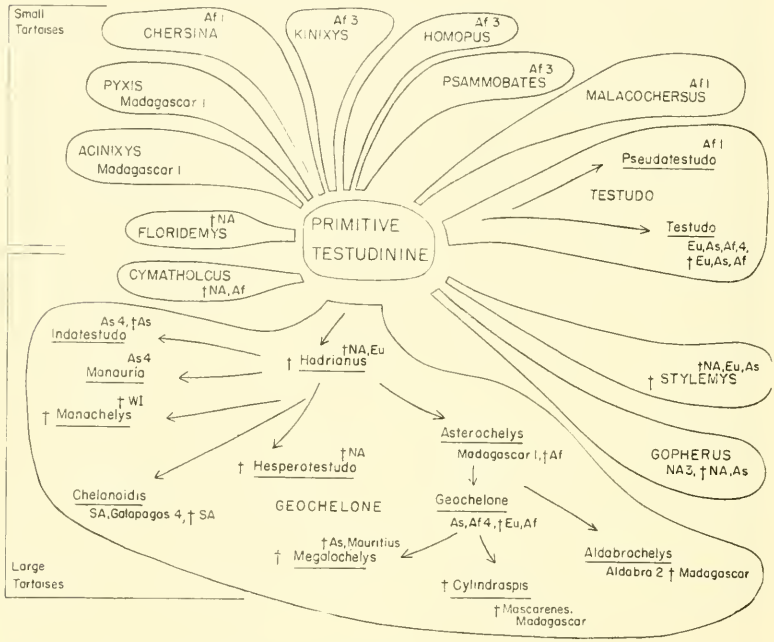


Fig. 8. A dendrogram of testudinine relationships. Names in capitals are those of full genera. Names underlined are those of subgenera as recognized in this revision. With each subgenus or genus is given its range and the number of Recent species, if any. The symbol † indicates an extinct form.

(P. Washer del.)

temporal region always emarginate posteriorly; temporal arcade rarely interrupted by absence of the postorbital; quadratojugal typically well developed, never absent, never in contact with

maxilla; jugal entering orbit; quadrate usually enclosing stapes; surangular not covered by dentary, often extensively exposed laterally.

Coracoids with median borders markedly widened; tuberosities of humerus tending to be approximated; trochanteric fossa of femur restricted by union of trochanters; epipodials very short; no digit with more than 2 phalanges, except in an extinct genus.

Carapace usually arched, high; rib heads often vestigial; neural bones primitively hexagonal, tending to become alternately quadrangular and octagonal, sometimes vestigial; of the inframarginal series only the axillaries and inguinals normally present.

Range. World-wide except for Australian region.

Remarks. The separation of the land tortoises into generic groups is not easy. Like the emydines they are a closely knit assemblage in which there has been much parallel evolution. Even more than in the emydines, it is difficult to distinguish between those characters that are merely convergent and those that may indicate natural divisions.

In a revision of African forms, however, the problem is a pressing and immediate one since nowhere else in the world do the tortoises achieve the diversity or the numbers of species that they have in Africa.

We have made a beginning by assembling the recognizable forms into species groups. Estimation of relationships at this level rests upon relatively secure foundations. With almost equal confidence we may proceed to the level of groups that may be termed subgenera, but above this uncertainties increase. In Figure 8 we have attempted a diagram of relationships between species-assemblages that are at least subgenera, and to which the available Latin names have been attached. We have included the evidence of fossil forms where these have been sufficiently well analyzed to be usable. Fortunately, in the testudinines, in contrast to the emydines, the fossil record approaches adequacy, at least in some periods and places.

In preparing Figure 8 we have considered the following as the characters which the primitive testudinine must have had.

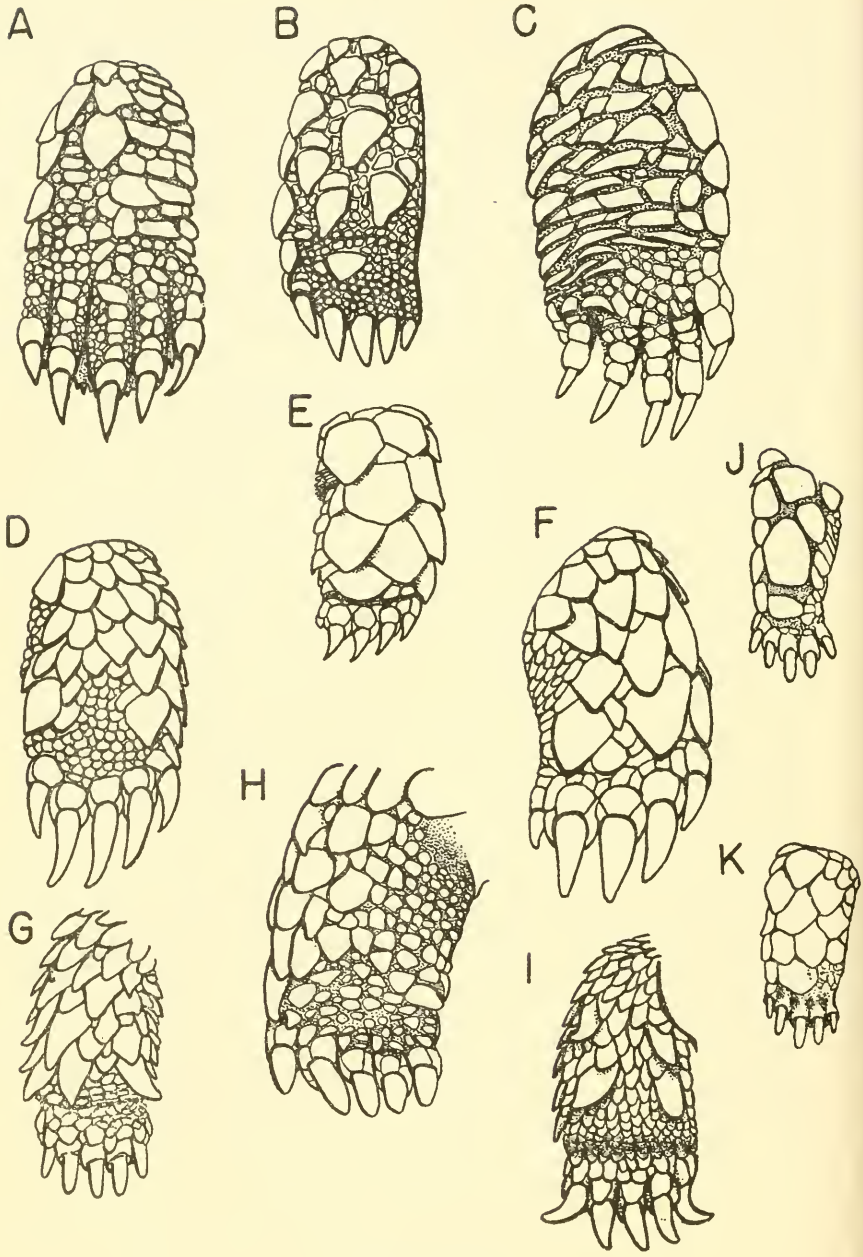


FIGURE 9

Osteological characters

1. Interval between ventral processes of the prefrontals only moderately widened.
2. Maxilla with triturating surface ridged, but premaxilla unridged.
3. Anterior palatine foramina small, concealed.
4. Temporal arcade strong.
5. Prootic well exposed dorsally.
6. Quadrate not enclosing stapes.
7. Surangular subequal in height to prearticular.
8. Fourth cervical centrum biconvex.
9. Anterior neurals hexagonal.
10. Suprapygal *one*, anterior to the vertebral-supracaudal sulcus.
11. Entoplastron anterior to humeropectoral sulcus.
12. Digital phalangeal formula 2, 3, 3, 3, 3.

External characters

1. At least prefrontal and frontal head scutes present.
2. Scales on forelimb numerous, not greatly enlarged.
3. Large femoral tubercles present.
4. Claws on forelimb 5, on hind limb 4.
5. Tail claw absent.
6. Carapace moderately convex.
7. Neither carapace nor plastron hinged.
8. Nuchal present.
9. Vertebrals not conical.
10. Vertebral keel very weak, lateral keels absent.
11. Supracaudal divided.

Fig. 9. Forelimb scalation in certain testudinids. *A, Clemmys caspica leprosa* (M.C.Z. 1894) (x 2); *B, Geochelone pardalis babcocki* (M.C.Z. 50304) (x 1); *C, Emys orbicularis* (M.C.Z. 5189) (x 1⅓); *D, Testudo hermanni* (M.C.Z. 3063) (x 1⅓); *E, Testudo kleinmanni* (M.C.Z. 5081) (x 2); *F, Testudo graeca graeca* (M.C.Z. 1497) (x 1⅓); *G, Malacochersus tornieri* (N.R. Stockholm), Njoro, (x 1); *H, Chersina angulata* (M.C.Z. 3998) (x 1); *I, Malacochersus tornieri* (M.C.Z. 30003), Mangasini, (x 1); *J, Psammobates t. trimeni* (M.C.Z. 42227) (x 1); *K, Psammobates t. tentorius* (M.C.Z. 21332) (x 1).

(P. Washer del.)

12. Submarginal scute absent.
13. Gular area but slightly produced or thickened.
14. Gulars paired.
15. Anal notch moderate.

Most of these characters are primitive emydine and are inferred to be also primitive testudinine on the well-grounded theory that the Emydinae are ancestral to the Testudininae. In several instances where there is a good fossil record for a tortoise lineage, it is possible to observe a shift in these characters from

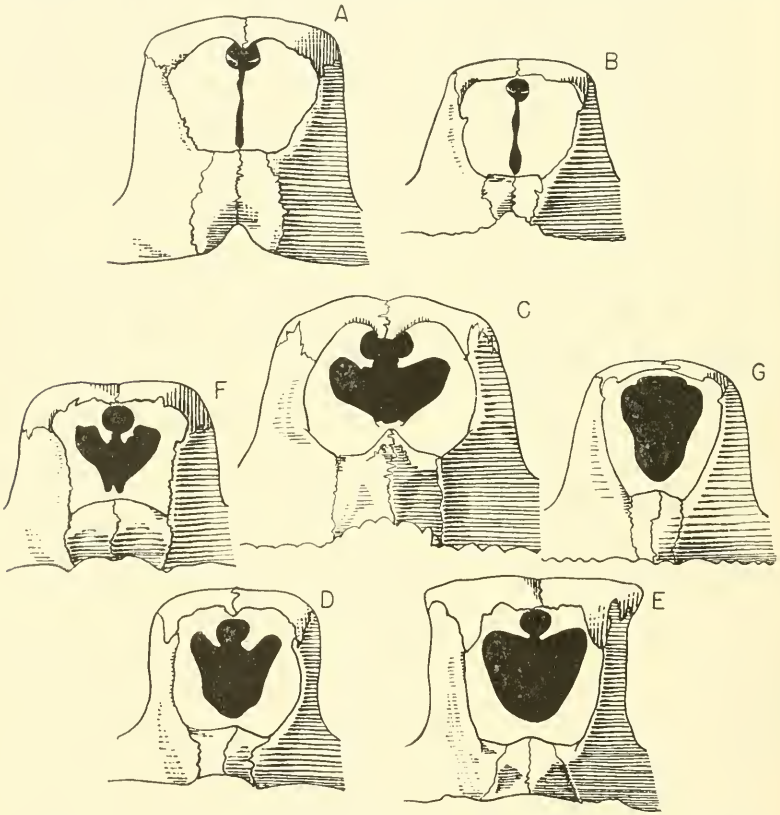


Fig. 10. Interprefrontal space in African testudinids I. *A, Clemmys caspica leprosa* (M.C.Z. 2210); *B, Emys orbicularis* (A.M.N.H. 74604); *C, Geochelone pardalis babcocki* (A.M.N.H. 7203); *D, Testudo graeca graeca* (M.C.Z. 4485); *E, Testudo kleinmanni* (Yale Mus. 662); *F, Malacochersus tornieri* (A.M.N.H. 45081); *G, Chersina angulata* (A.M.N.H. 50725).

(P. Washer del.)

the earlier to the later members, e.g. from the emydine hexagonal neural pattern to the advanced testudinine octagonal *cum* quadrilateral condition.

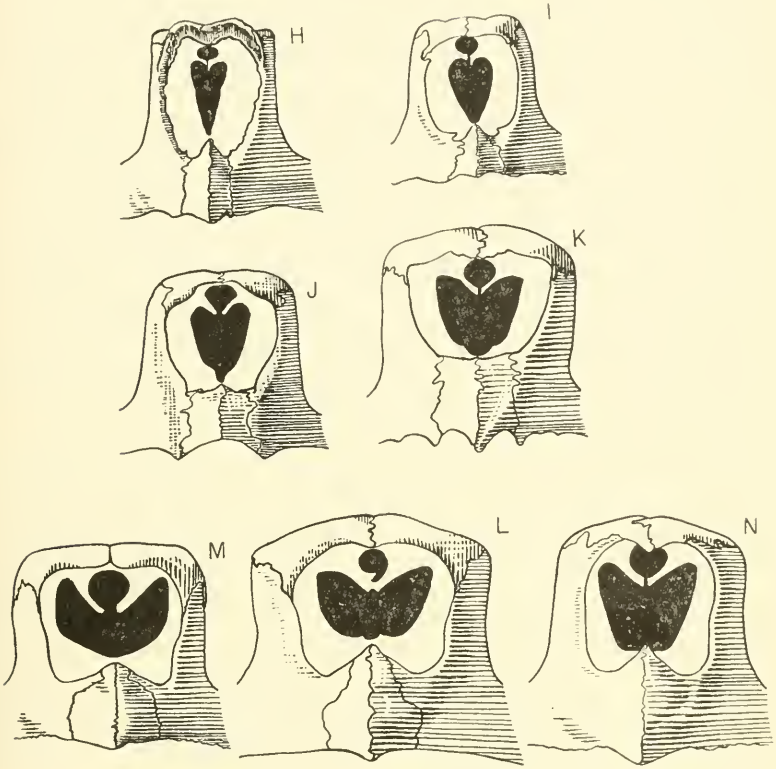


Fig. 11. Interprefrontal space in African testudinids II. *H, Psammobates t. tentorius* (M.C.Z. 3465); *I, Psammobates t. verroxii* (M.C.Z. 21330); *J, Homopus boulengeri* (A.M.N.H. 7107); *K. Homopus areolatus* (A.M.N.H. 17792); *L, Kinixys erosa* (A.M.N.H. 69727); *M, Kinixys homeana* (A.M. N.H. 50725); *N, Kinixys b. belliana* (A.M.N.H. 10029).

(P. Washer del.)

All the osteological characters listed are clearly primitive emydine, with the possible exception of the small, concealed, anterior palatine foramina. The latter feature is considered

primitive for testudinines because of its more frequent occurrence in forms regarded as primitive on other grounds. Similarly we treat as primitive for testudinines certain kinds of scutellation unknown in emydines, e.g. complex head scutellation with supranasals, prefrontals and frontals.

No living tortoise exhibits the whole complex of characters[1] here considered primitive. Rather, the members of the Testudininae display various combinations or *mosaics* of primitive and advanced characters, characteristic for each subgroup or lineage.[2]

Superficially considered, the tortoises give a great overall impression of homogeneity — far greater than that provided by the emydines. But when all the evidence is considered and particularly that of the rather good fossil record, it is apparent that this homogeneity is primarily one of *trends* and only secondarily of realized conditions. The records seem to indicate there has been no single sequence, but rather a number of starts from a single point of departure.

The development of advanced characters in the separate lines has been quite independent; the characters have been neither consistently synchronous in appearance nor consistently consecutive nor in any evident way correlated. Each lineage appears to be characterized by the timing of initiation of the several advanced characters, and some lineages indeed are still primitive in certain aspects today, some in others. A discussion of the paleontological evidence supporting these conclusions is not pertinent here and will be presented separately by one of us (EEW). It is however with these considerations in mind that we have framed our diagrams of relationship and based our decisions as to generic rank.

[1] In our generic definitions we have used many, but not all 27, of the listed characters, or their advanced alternatives. Certain of them have proved too variable within groups, or even within species, to be of taxonomic value. We have also preferred osteological to external characters.

[2] Anyone desiring to check these statements is referred to our numerous figures. Figures 10 and 11 show the condition of the interval between the ventral processes of the prefrontals in most of the African Testudinidae. Figures 19 and 22 furnish examples of head scutellation. Figures 9, 39 and 44 illustrate types of limb scutellation. Figure 12 shows the suprapygal area. Under each genus will be found additional illustrations of, at least, major skull and shell characters. With regard to the latter a warning is necessary. There has been neither the opportunity nor the desire to figure "typical" specimens. Both age and individual variations have been drawn when present in the specimen depicted, and attention has been directed only to the more striking peculiarities or abnormalities.

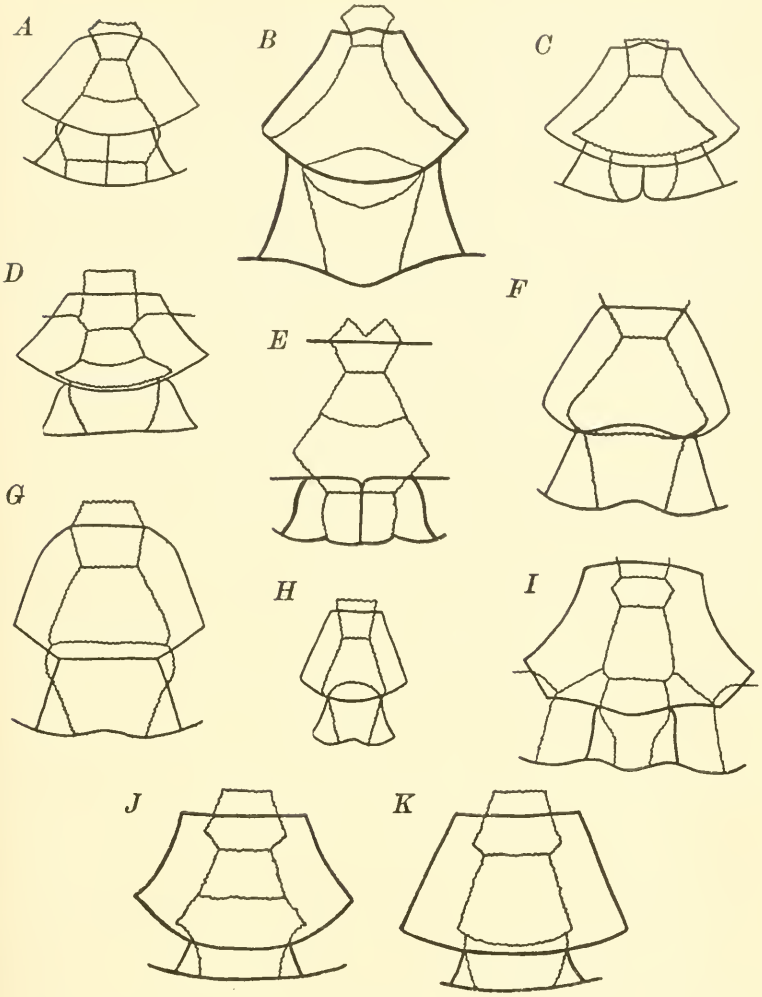


Fig. 12. Pygal patterns in testudinids (diagrammatic). *A, Clemmys caspica leprosa* (Pygal pattern differs within the genus *Clemmys* as currently recognized); *B, Geochelone pardalis babcocki; C, Emys orbicularis; D, Testudo graeca graeca; E, Malacochersus tornieri; F, Psammobates tentorius tentorius; G, Chersina angulata; H. Homopus signatus; I, Kinixys erosa; J, Acinixys planicauda; K, Pyxis arachnoides.*

(P. Washer del.)

In summary, we have come to the following conclusions:

The assemblage that has the Eocene subgenus †*Hadrianus* as its base is a natural grouping and one that appears to us to extend back to the very base of the tortoise line. We have adopted the generic name *Geochelone* for the whole of this rather homogeneous group.

†*Stylemys*[1] and *Gopherus* share a unique specialization — the median premaxillary ridge — and thus clearly belong together but their differences (i.e. in phalangeal formula) point to a very ancient separation at practically the emydine level (see below, p. 255 ff), and we therefore regard them as two quite distinct genera.

Testudo in the strict sense (with *T. graeca* Linnaeus as the type) and *Pseudotestudo* new subgenus (*T. kleinmanni* Lortet type) seem appropriately bracketed together by certain very singular specializations (prootic completely concealed by the parietal,[2] and plastron posteriorly hinged in one or both sexes), but *Pseudotestudo*, which has not been separated from *Testudo* previously, shows some amazing differences in skull structure (see p. 259 and Figs. 20, 24). There are, fortunately, transitional forms in this series and the unity of the genus appears satisfactorily established. The record demonstrates that this lineage is as ancient as that of *Geochelone* (†*Testudo comptoni* of the Eocene of England, see pp. 353 ff below).

For the groups so far mentioned there has been, happily, a fossil record. For the diverse forms of the Ethiopian region there is no such aid. We have proceeded here on the strict ground of degree of morphological difference, influenced, however, by the extra-African evidence that only modest morphological difference may mean very ancient divergence.

We shall argue below that *Acinixys*, *Pyxis*,[3] *Psammobates*, *Chersina*, *Homopus* and *Kinixys* are related. The individual

1 As a matter of convention throughout this paper every extinct genus or species is preceded by the symbol †.

2 This character was first noticed by Baur (1892), who was also the first to point out the "*Testudo leithii*" (i.e. *kleinmanni*) characters that have led us to separate it as a subgenus.

3 *Pyxis* Bell, 1825, is used rather than *Bellemys* Williams, 1950, 1952, in as much as the supposedly preoccupying name *Pyxis* Chemnitz 1784 is not binomial, and the next use of the name (Humphreys in the "Museum Calonnianum" 1797) has now been outlawed by ruling of the International Commission on Nomenclature (Decision 51).

specializations of each, however, are so marked that we regard each as constituting a separate genus. *Malacochersus* we have found difficult to place, its relationships quite obscure; we suggest that it has branched off at or very near the base of the testudinine series, and we have therefore retained it as a genus also.

Shown on the relationship diagram for the sake of completeness, are two fossil forms of uncertain position. Though imperfectly known, on present evidence they appear to be quite

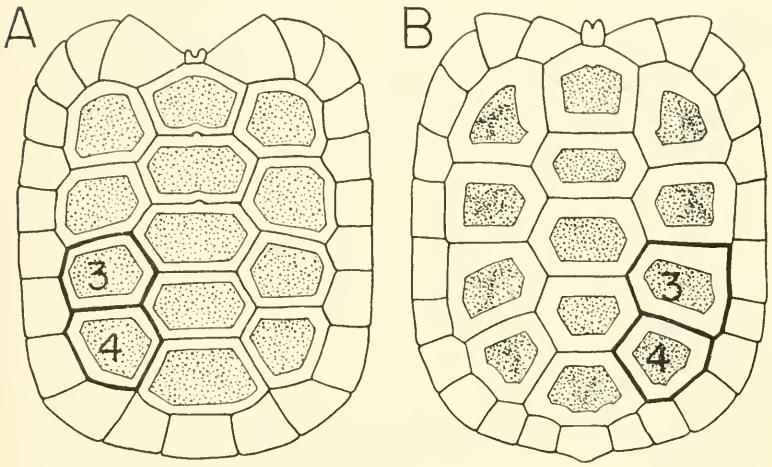


Fig. 13. Third and fourth costals of *Kinixys* for comparison with those of *Homopus*. *A*, *Kinixys b. belliana* (M.C.Z. 40008); *B*, *Homopus boulengeri* (M.C.Z. 42231).

(P. Washer del.)

isolated. A few other fossil genera — †*Achilemys* Hay, †*Cheirogaster* Bergounioux, †*Sinohadrianus* Ping — listed in Williams (1952), are impossible to place at this time. Further comment on the African genera will be found under each genus.

Key to the Genera of Testudininae in Africa[1]

1. Carapace hinged posteriorly *in adults,* usually between 7th and 8th marginals; outer side of fourth costal markedly wider than outer side of third (*in all ages*) (cf. Fig. 13). Range: Africa from 17° north to Bechuanaland and Natal ..... *Kinixys* Bell (p. 374)
   Carapace without hinge; outer side of fourth costal subequal to, or smaller than, outer side of third ..... 2.
2. Gular single, strongly projecting. Range: South Africa ..... *Chersina* Gray (p. 342)
   Gulars paired ..... 3.
3. Carapace very flat, flexible, fenestrated; neural bones reduced; plastron with a great fontanelle at all ages. Range: arid areas of Kenya and Tanganyika ..... *Malacochersus* Lindholm (p. 283)
   Carapace more or less convex, rigid, solid; neural bones unreduced; plastron with a fontanelle only in hatchlings ..... 4.
4. Maxilla unridged; anterior neurals hexagonal or quadrilateral ..... 5.
   Maxilla ridged (except in *Testudo kleinmanni* of Egypt); anterior neurals octagonal and quadrilateral ..... 6.

1 Some divergence of opinion occurs with regard to the advisability of breaking up *Testudo* into several genera — first attempted by Fitzinger (1835) and more recently by Hewitt (1931: 1933b). Uninfluenced by either of these authors, my colleague, Dr. E. E. Williams, is fully convinced by his own studies that certain structural differences indicate so early a divergence among the several groups as to justify their recognition as full genera. He considers their numerous similarities, when not due to common ancestry, are attributable to parallel evolution or due to convergence. Assumptions as to which characters reflect close affinity, and which are to be discarded as subsequent convergences, seem somewhat speculative to me in view of the fact that the fossil history of five of the seven suggested genera is completely unknown.

More impressed than my colleague by the many similarities (which may be seen by comparing the several generic descriptions), I take a more pragmatic view of the purposes of nomenclature. A multiplicity of genera that are based on single characters, or aggregations of characters that in themselves may be subject to variation, and sometimes difficult to observe or evaluate, tends to nomenclatorial confusion. For an instructive example of the extent to which genera-making can burden posterity, one has only to turn to the 28 synonyms of *Trionyx* (cf. p. 420).

Fragmentation of *Testudo* offers the advantage of separating into groups those species whose characters are believed to indicate close affinities. On the other hand, this result can be achieved by treating such groups as subgenera, an arrangement that has the additional advantage of emphasizing their over-all relationship, though to this my colleague's views naturally prevent him from subscribing (cf. Fig. 8). To me, as a working herpetologist, the desirability of maintaining as stable a nomenclature as possible outweighs the advantages of emphasizing a new theory of phylogeny (that may not find general acceptance or have to be set aside when more is known of the fossil history involved) by raising the several groups to full generic status. In the conservative view, *Geochelone, Psammobates* and *Chersina* would be retained as subgenera of *Testudo.*

Possibly this attitude is a mistaken one, so for the purposes of this revision I defer to a current trend in herpetology. This is done in the confident belief that — as increasing knowledge reveals the disadvantages of a multiplicity of genera that are difficult to define — in due course there will be a return to the larger units as is even now occurring in South African ornithology following an extended period of nomenclatorial chaos. A.L.

5. Carapace somewhat depressed; vertebral shields never conical; each gular usually broader than long (cf. Fig. 14); anterior palatine foramen large, conspicuous; maxillary bone not entering roof of palate. Range: South Africa ..... *Homopus* Duméril and Bibron (p. 352)

   Carapace rather convex; vertebral shields sometimes conical; each gular usually as long or longer than broad; anterior palatine foramina small, concealed; maxillary bone entering roof of palate. Range: South Africa ..... *Psammobates* Fitzinger (p. 294)

6. Supranasal scales present; nuchal scale present; femoral tubercles absent or only 1; suprapygal single or divided transversely; posterior lobe suprapygals 2, a larger anterior one embracing a smaller posterior one of plastron (in life) more or less clearly movable in one or both sexes; prootic usually concealed dorsally by the parietals. Range: North Africa ..... *Testudo* Linnaeus (p. 254)

   Supranasal scales absent; nuchal scale absent; femoral tubercles 2 or 3; suprapygals 2, a larger anterior one embracing a smaller posterior one (cf. Fig. 12B); posterior lobe of plastron never movable; prootic usually well exposed dorsally. Range: Tropical and South Africa.... *Geochelone* Fitzinger (p. 221)

Genus GEOCHELONE Fitzinger

1835. *Geochelone* Fitzinger, Ann. Wiener Mus., 1: pp. 111, 112, 122. Type: *Testudo stellata* Schweigger = *T. elegans* Schoepff (designation by Fitzinger: 1843).

1872c. *Centrochelys* Gray, Appendix Cat. Shield Rept. Brit. Mus., p. 5. Type: *Testudo sulcata* Miller (by monotypy).

1873b. *Stigmochelys* Gray, Hand-List Shield Rept. Brit. Mus., p. 5. Type: *Testudo pardalis* Bell (by monotypy).

1933b. *Megachersine* Hewitt, Ann. Natal Mus., **7**, p. 257. Genotype: *Testudo pardalis* Bell (by original designation).

Definition. Skull with triturating surface of maxilla strongly ridged; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina small, concealed in ventral view; prootic typically well exposed dorsally and anteriorly; quadrate usually enclosing stapes; surangular subequal in height to prearticular; neck with second, third or fourth centrum biconvex.

Carapace never hinged; typically the anterior neurals alternately octagonal and quadrilateral; outer side of third costal scute about as long as, or longer than, that of the fourth; no submarginal scute; suprapygals 2, the anterior larger, bifurcat-

ing posteriorly to embrace the smaller posterior element, which (in post-Eocene forms) is crossed near its middle by the sulcus between the fifth vertebral and the supracaudal.

Plastron not hinged; gular region more or less thickened and produced; gulars single or paired, longer than broad.

Range. Galapagos Islands; South America; Africa; Madagascar and other islands of the Indian Ocean (including Ceylon); southeastern Asia (including India).

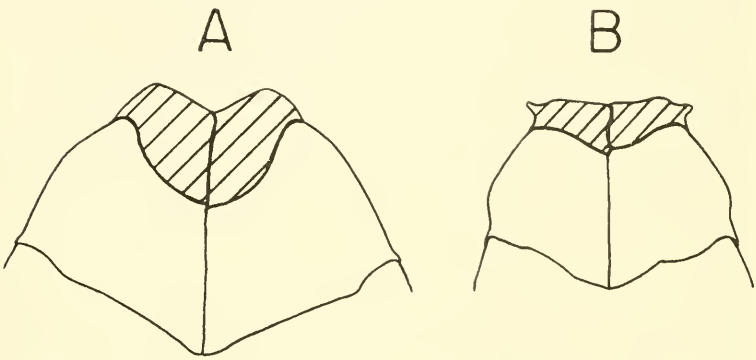


Fig. 14. Typical shape of gular scutes in *Psammobates* for comparison with those of *Homopus*. *A*, *Psammobates t. verroxii* (M.C.Z. 42222); *B*, *Homopus areolatus* (M.C.Z. 17524).

(P. Washer del.)

Fossil record. Well represented in the Tertiary and Pleistocene of North America and the Tertiary of Europe; known from the Oligocene and Pliocene of Asia; from the Oligocene and Miocene of Africa; recorded in South America only since the Miocene, and in the West Indies from the Pleistocene.

Remarks. The genus *Geochelone* tends to large size. In carapace length some fossil and Recent species may exceed a meter in length and none attains to less than 250 mm.

Characteristic of this genus is the fact that the shell takes on certain specializations early in its phyletic history. Earliest of these are a thickened, produced gular region and the peculiar pygal pattern with the first suprapygal embracing a smaller second one, both already present in †*Hadrianus* of the Eocene.

TABLE 3

Characters of the subgenera of *Geochelone:* there are additional habitus features.[1]

Subgenus	Living species	Nuchal present	Supra-caudal divided	Neurals hexagonal	First dorsal vertebra elongate	Gulars single	Gulars bifureate	Pectorals narrowed	Nares expanded vertically	Postotic fenestra concealed	Entoplastron crossed by humeropect-oral suleus
†*Hadrianus*	0	+	+	+	—	—	—	—	—	—	—
Asterochelys	2	+	—	—	—	±	—	—	—	—	—
Aldabrachelys	2	±	±	—	—	—	—	—	+	—	—
Geochelone	4	—	—	—	—	—	—	+	—	—	—
Cylindraspis	2	—	—	—	—	+	—	—	—	—	—
†*Megalochelys*	0	—			—	—	+	—			—
Manouria	2	+	+	—	—	—	—	+	—	+	—
Indotestudo	4	+	—	—	—	—	—	—	—	—	+
†*Hesperotestudo*	0	+	—	—	—	—	—	+	—	—	±
Chelonoidis	4	—	—	—	—	—	—	—	—	+	—
†*Monachelys*	0				+				—	—	—

1 For types and content of subgenera here recognized (except *Aldabrachelys* nov.) see Williams (1952).
† Indicates a fossil form or group.

The alternate octagonal-quadrilateral neural pattern arises a little later, but even in †*Hadrianus* one of the neurals may sometimes be octagonal and several of them are often hexagonal short-sided behind. The latter conditions are intermediate, indicating the establishment of a trend which, at least in North America, culminated in the perfected pattern in the Oligocene. An octagonal-*cum*-quadrilateral pattern for the anterior neurals is now very characteristic of the genus, though by no means invariable.

Other shell specializations occur irregularly within the genus. The nuchal scute is lost in many species. The supracaudal is usually single in post-Eocene subgenera with the exception of *Manouria*. The pectoral scutes tend to become narrowed, moderately so in the African species, to an extreme degree in the typical members of the fossil American subgenus †*Hesperotestudo*. In *Cylindraspis*, and independently in *Asterochelys yniphora*, the gulars have fused to form a single scute, while in the subgenus †*Megalochelys* the gular region becomes not merely produced but strongly bifurcate. Variation in height of shell occurs also (contrast *G. radiata* and *G. emys*) as well as striking differences within a species (cf. *G. pardalis*). The humeropectoral sulcus crosses the entoplastron well anteriorly in the subgenus *Indotestudo*, in which this feature was established early (†*G. kaiseni*[1] and †*G. nana*[1] of the Oligocene of Mongolia). The same character occurs irregularly in a number of fossil species elsewhere, e.g. †*G. wintensis*[2] and †*G. costaricensis*[3] of North America.

In contrast to the shell, the skull in most of the subgenera of *Geochelone* is remarkably primitive (for a testudinine) and surprisingly uniform. However, there is a tendency, several times repeated, for a downgrowth of the opisthotic to more or less conceal the postotic fenestra in posterior view. Apart from this the only striking modification occurs in the Seychelles-Aldabra tortoises and †*G. grandidieri* of Madagascar. In these the external naris is extraordinarily extended dorsoventrally in conjunction with a distortion of the whole front of the skull, giving

1 C. W. Gilmore, 1931, Bull. Am. Mus. Nat. Hist., **59**, pp. 213-257.

2 C. W. Gilmore, 1915, Mem. Carnegie Mus., **7**, pp. 101-161.

3 A. Segura, 1944, Escuela de Farmacia, Guatemala, **6**, Nos. 73-74, pp. 9-29; Nos. 75-76, pp. 16-25; Nos. 77-78, pp. 13-24.

the latter a bulbous appearance. Since this modification appears to be quite as distinctive as any of the features, or combinations of features, that distinguish subgenera of *Geochelone,* and since the minor lineage involved seems to be quite a distinct one, we here propose a new subgenus for *gigantea, sumeiri* and †*grandidieri,* to be called:

ALDABRACHELYS new subgenus

Type species: *Testudo gigantea* Schweigger

Definition. External naris higher than wide; quadrate enclosing stapes or not; postotic fenestra not concealed in posterior view; nuchal present or absent; typically the anterior neurals alternately octagonal and quadrilateral; first dorsal vertebra short and stout; supracaudal divided or undivided; gulars paired but not divergent; entoplastron not crossed by the humeropectoral sulcus.

Range. Aldabra and Madagascar.

The continental African species of *Geochelone* belong to the nominate subgenus, defined as follows:

Subgenus GEOCHELONE Fitzinger

1835. *Geochelone* Fitzinger, Ann. Wiener Mus., 1, pp. 108, 112, 122: as a subgenus. Type species: *Testudo stellata* Schweigger = *T. elegans* Schoepff.

Definition. External naris not higher than wide; quadrate enclosing stapes; postotic fenestra not concealed in posterior view; nuchal absent; anterior neurals alternately octagonal and quadrilateral; first dorsal vertebra short and stout; supracaudal undivided; gulars paired but not divergent; entoplastron not crossed by humeropectoral sulcus.

Distinguishing marks. The African members of this subgenus are easily distinguished from other African tortoises. They are the only ones with 2 or 3 subconical tubercles on the hinder side of each thigh, and are by far the largest in adult size.

Range. Africa; Ceylon; India and Burma.

Fossil record. Not known fossil with any certainty except in the Tertiary of Europe. Probably the fossil giant tortoises of

the islands of Malta, Minorca and Teneriffe belong to this subgenus.

Remarks. The living members of the subgenus divide into two species groups, an Asian one consisting of *G. elegans* and *G. platynota*, and an African one comprised of *G. sulcata* and

Fig. 15. Locality records of *Geochelone* in East Africa north of the Equator.

(P. Washer del.)

G. pardalis. The African species are much the larger and differ also in not possessing the tail claw which is present in the Asian forms. Both species groups appear to have been present in Europe during the Tertiary.

The large tortoises of Africa present a relatively simple picture. The largest and most northerly species, *G. sulcata,* is confined to a rather arid belt extending from Senegal to Eritrea, consequently inhabiting mostly the Sudanese subprovince of the Savannah Province of botanists, but also present in the northern portion of the Northeastern subprovince. *G. pardalis babcocki,* relatively uniform in all its characters, occurs southwards from the southern Sudan and Ethiopia throughout most non-forested areas of the eastern half of the continent, westwards into Angola and the northern half of Southwest Africa. Known from very few specimens is *G. p. pardalis,* which occupies, or did occupy (it is perhaps now extinct), a very limited region in western South Africa.

Though available evidence shows *G. sulcata* to be allopatric to *G. pardalis* they have always been separated specifically, a view we see no reason to reverse. *G. sulcata* differs more from the two *pardalis* forms than do the latter from each other. The frontal scute characteristic of *sulcata* is lacking in all the *pardalis* we have seen. While the pale color of *sulcata* is approached by individual *pardalis*, especially those from arid regions that have lost most of their black pigmentation, no *pardalis* is known to us in which the black flecking is entirely absent. More significant is the striking difference in convexity displayed by the much larger *sulcata* when contrasted with its nearest neighbor, *pardalis babcocki.*

The situation in regard to the two subspecies of *G. pardalis* is sufficiently confused to require some extended discussion. The subspecies *babcocki* was separated from the typical race by one of us (Loveridge:1935c) when he discovered that two specimens from Southwest Africa in the collection of the Museum of Comparative Zoology did not correspond to the form known to him in East Africa. Photographs of these two Southwest African tortoises are presented here for the first time and contrasted with East African material. The markings of the adults

TABLE 4

Characters of the African species and subspecies of *Geochelone*

Character	*sulcata*	*p. babcocki*	*p. pardalis*
frontal scute	usually present and large	absent	absent
convexity of carapace	flattened dorsally	very convex	flattened dorsally
shape of gular region	somewhat produced and notched	not or but slightly produced, not or but slightly notched	slightly produced, shallowly notched
enlarged scales on forelimb	juxtaposed	usually not juxtaposed	not juxtaposed
color of adult	uniform horn color	yellow, richly variegated with black; or rarely mostly yellow	yellow to greenish variegated with black
color of hatchling	pale yellow, the dorsal shields edged with brown; plastron pure yellowish white	light brown, the dorsal shields broadly edged with black and typically containing a red-bordered areola within which is a *single* spot centrally located and usually united to the posterior areolae, *or*, in the extreme north, the central spot flanked by two lateral ones[1], plastron as in *p. pardalis.*	dull yellow, the dorsal shields narrowly edged with black and containing a red-bordered areola within which is a *pair* of spots separated by a light vertebral line: plastron dull yellow, sutures of the shields more or less margined with black.
maximum size recorded	762 mm.	585 mm.	432 mm. (type)

1 As in a specimen from Mongalla, Sudan, photographed for us by Dr. J. Eiselt of the Vienna Museum; also an Ethiopian tortoise figured by Vaillant (1904a) as *calcarata.* In some Kenya hatchlings the areolar spots may be altogether absent.

are probably indistinguishable, but in juveniles the marked flattening of the carapace is usually correlated with a color pattern so distinctive that the *nomen nudum biguttata*[1] was proposed in a footnote by Cuvier (1829:10; Duméril and Bibron: 1835).

Although twenty years have elapsed since the description of *p. babcocki,* it is still difficult to clearly define the ranges of the two forms because of the paucity of *p. pardalis* material with good locality data. A number of specimens at the British Museum (measured at the time *babcocki* was described) appear to belong to *p. pardalis,* but are labeled only "South Africa." In addition to these the only specimens definitely known to us are the following: Bell's type of *pardalis* with the locality "Cape of Good Hope"; the adult shell (M.C.Z. 16713) labeled as from Kolmanskop (Dr. W. Beetz coll.); a hatchling (M.C.Z. 22473) from Aroab (W. S. Brooks coll.); the young specimen figured by Duerden (1907b:fig. 7) and Hewitt (1937e:pl. i, fig. 2; pl. ii, figs. 1-2).[2]

We have also hesitantly assigned to the nominate race the Archer tortoise from Keetmanshoop because that locality is so near to Aroab, and, because of their proximity to the type locality of *pardalis,* the Delalande specimens from Oliphants River, Cape Province. However, one Delalande tortoise in the Paris Museum, labeled as the type of *biguttata* Cuvier, with locality "Cap," is an intergrade — being as convex as *p. babcocki* but with the juvenile pattern of *p. pardalis.*

For further remarks on this subject see the footnote on p. 250.

Key to the Species and Subspecies of Geochelone *in Africa*

1. Carapace horn-color or brownish, *uniform;* frontal shield usually present, large. Range: Eritrea and Ethiopia west to Senegal ..... *sulcata* (Miller) (p. 230)

   Carapace yellow or olive more or less richly variegated with black; frontal shield absent 2

2. Carapace distinctly convex, its height being included in its length (in a straight line) from 1.61 to 2.11 times; vertebral shields of young with a *central* black spot. Range: Anglo-Egyptian Sudan and Ethiopia

[1] Erroneously cited as *T. bipunctata* by Gray (1831c:12).

[2] Thanks to Dr. Robert Mertens, we have a photograph of two additional specimens from Rehoboth, south of Windhoek, Southwest Africa.

south to Natal, west through Cape Province to Southwest Africa (where it meets with the typical form, but is dominant north of 27° S.) and southern Angola .....*p. babcocki* (Loveridge) (p. 235)

Carapace distinctly flattened dorsally, its height being included in its length (in a straight line) from 2.02 to 2.62 times; vertebral shields of young with a pair of lateral black spots *separated by a light longitudinal line.* Range: southern Southwest Africa (in former times possibly extending south to the Cape Peninsula, as the type locality was said to be the Cape of Good Hope) .....*p. pardalis* (Bell) (p. 251)

Geochelone sulcata (Miller)[1]

1780. *Testudo sulcata* Miller, Icones animalium et plantarum (Various Subjects of Natural History . . .), pl. xxvi: "India occidentali" (in error).
1789. Gmelin, 1045.
1792. Schoepff, p. 156 (German ed.).
1796. Shaw, *in* Miller (vide supra), 53, pl. xxvi.
1800. Bechstein, *in* Lacépède, 346.
1801. Schoepff, p. 135.
1802b. Daudin, 313.
1802. Shaw, 39.
1812. Schweigger, 323, 452.
1814. Schweigger, 53, 55 (reprint of 1812).
1831c. Gray, 11.
1835. Duméril and Bibron (part), 74, pl. xlii, figs. 1-1a.
1844. Gray, 7.
1845b. Rüppell, 297.
1851. Guichenot, 189.
1855. Gray, 9.
1860. Duméril, 162.
1862a. Strauch, 78.
1865. Strauch, 22.
1870a. Steindachner, 326.
1872b. Gray, 4, *in* Sowerby and Lear, pls. xvii-xviii.
1884a. Rochebrune, 13 (ignored).
1890. Strauch, 52.
1905. Barbier, 83, pl. iii.
1912. Siebenrock, 214, fig. 2.
1924a. Werner, 263, figs. —.
1928. Flower, 654, figs. 1-2.

[1] *Testudo Schöpfi* Fitzinger (*nom. nud.*), 1826, sometimes referred to the synonymy of *sulcata,* was subsequently synonymized by Fitzinger with *Kinixys erosa.*

1929. Flower, 32.
1937a. Flower, 9.
1784. *Testudo calcarata* Schneider, Samml. Vermischt. Abhandl. Zool. p. 317, pl. — (based on Miller's figure of *sulcata*).
1835. Rüppell, 4.
1880c. Vaillant, 33, 88, pl. xxvi, fig. 3.
1889a. Boulenger, 159.
1891. Prato (not seen).
1893. Trimen, 79.
1904a. Vaillant (part), 186 (fig. of juv. is *p. babcocki*).
1906. Kammerer, 48, fig. 7.
1906a. Siebenrock, 821.
1908c. Kammerer, 769, figs. 6-7.
1908. Werner (1907), 1826.
1909a. Siebenrock, 521.
1911a. Masi, 34.
1914a. Pellegrin, 122, pl. i, fig. 2.
1925b. Flower, 924.
1928b. Scortecci, 334.
1930a. Scortecci, 215.
1950. Williams, 550.
1820. *Chersine calcarata* Merrem, 32.
1831c. *Testudo radiata* var. *senegalensis* Gray, Syn. Rept., p. 4; Senegal.
1836. *Geochelone sulcata* Fitzinger, 122.
1855. *Geochelone senegalensis* Fitzinger, 251.
1869c. *Peltastes ? sulcatus* Gray, 173.
1870c. Gray, 656.
1870e. Gray, 12.
1873b. *Centrochelys* (*Peltastes*) *sulcatus* Gray, 13.
1873c. Gray, 725.

Further citations of "*sulcata*" and "*calcarata*" will be found under *Geochelone p. babcocki*.

Synonymy. The use of the name *sulcata* has been dealt with at some length by Siebenrock (1912:214). As the copy of Miller's work in the library of the Museum of Comparative Zoology lacks the pertinent part of the text, and plate xxvi bears no name, we appealed to H. W. Parker for help in verifying Siebenrock's conclusions. Dr. Parker replied that though plate xxvi in the British Museum copy is also unnamed, there is a list of plates which states:

"Tabula XXVI

Fig. A. *Testudo sulcata.* Lin. Syst. Nat. Classis III. Ordo I. Genus CXIX. Spec. Habitat in India occidentali.
B. Pars inferior.
C. Caput magnitudine naturali."

Thus no doubt remains as to *sulcata* being the correct name to apply to this species. Furthermore, Parker points out that plate xxvi appeared in Part 5, which, according to Sherborn and Iredale (1921, Ibis:302-309) was published apparently in 1779 or 1780.

Common names. Spurred Tortoise (preferred); Grooved Tortoise (Flower); *abu gatta* (Arabic in Kordofan, *fide* Fitzinger, who translates it as "father of covers"); *abu gefne* (Arabic in

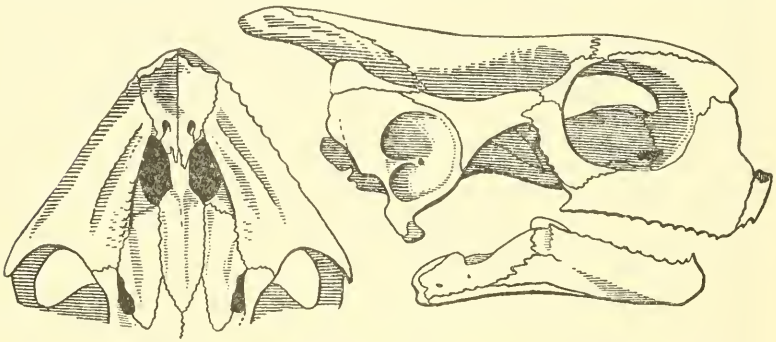


Fig. 16. Skull of *Geochelone sulcata* (B.M. 1904.7.28.1).
(S. McDowell del.)

Dongola: Rüppell); *gafot* (at Massaua: Rüppell).

Illustrations. For most people Miller's fine plate (1780) and its reproductions will be unavailable, but Sowerby and Lear's (1872) (our Plate 1) are equally good. Werner (1924a) and Flower (1928) have figured the young.

Description.[1] Beak weakly hooked, edge of jaws strongly dentate; prefrontal large, divided longitudinally; frontal usually large, rarely broken up; remaining upper head shields small, irregular; forelimb anteriorly with large unequal, *juxta-*

1 Based chiefly on the head, limbs and shell of an adult ♀ (M.C.Z. 11975) from Katsina Emirate; together with notes on British Museum material as of 1953, two without data in the A.M.N.H., and one without data in the C.N.H.M.

posed or imbricate scutes, forming 3-6 longitudinal and 6-7 transverse series from elbow to outer claw; claws 5; posterior side of thigh with 2-3 large conical tubercles; heel with large, conical, spurlike, bony tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace flattened dorsally, sides descending abruptly, deeply notched in nuchal region, anterior and posterior margins reverted and serrated, not more than twice as long as deep; dorsal shields concentrically grooved; nuchal absent; vertebrals 5, not convex, the second, third and fifth much broader than long, broader than the costals; costals 4, not forming an angle with the marginals; marginals 11; supracaudal undivided.

Front lobe of plastron somewhat produced and bifid; gulars paired; pectorals very narrow, their anterior border usually straight, widening abruptly towards the axillary notch; axillaries 2; outer moderate to small, inner minute; inguinals 2, outer large to moderate, inner small, meeting femoral; hind lobe deeply notched posteriorly, angular or crescentic.

Plastral formula: Abd>h>f>g>or=p>an.

Color. Carapace of juvenile (50 mm.[1]) pale yellow, the shields with narrow brown sulci. Plastron yellowish white.

Carapace of adult brownish to horn color, uniform. Plastron yellowish, uniform.

Size. Carapace length of ♀ (M.C.Z. 19975) from Katsina Emirate, 670 mm., breadth 470 mm., height 270 mm. Apparently exceeded by that of a specimen mentioned below.

The carapace of a young ♂ hatched at Giza Zoo on 5.x.10, was about 50 mm. long by 45 mm. broad at time of hatching. On 26.iii.28 this tortoise measured 762 mm. (30 inches) in length and weighed 184 lbs. (Flower:1928). The 800 mm. carapace from Eguei mentioned by Pellegrin (1914a) may have been measured over the curve.

Longevity. Two tortoises hatched at Giza Zoo on 5.x.10, lived for 19 years, 9 months, 26 days, and 20 years, 7 months, 22 days respectively, but were possibly surpassed by an adult ♂ measuring "28 inches across the shell" which had been in captivity "over 38 years" when presented to the London Zoo on 3.x.31. It died at Whipsnade on 19.xii.35 when reputedly over 42 years old (Flower:1937a).

[1] Cf. Flower (1928:654).

Enemies. The flesh of a Spurred Tortoise is "never eaten" by the natives, according to Rüppell (1835). However, his informants may have been Moslems.

Habitat. In the Sudan, according to Werner (1908:1826) *sulcata* extends no further south than Kordofan, being separated by the swamps of the Bahr el Gebel region from the range of *p. babcocki*, still known only from points south of Bor on the White Nile — i.e. about 5° N.

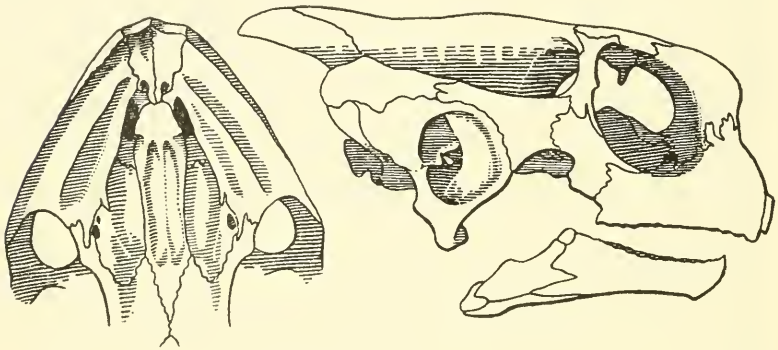


Fig. 17. Skull of *Geochelone pardalis babcocki* (A.M.N.H. 7703). Condylobasal length 81 mm.

(S. McDowell del.)

Localities. Sudan: Dongola;* Jebel Teiga, 30 miles west of Jebel Medob (B.M. specimen seen by E.E.W.); Kordofan; Omdurman (bought in market by Werner:1924a). *Eritrea:* Chenafena; between Cheren (Chire) and Mareb (Marembe) River;[1] Godolefassi; Massaua Coast. *Ethiopia:* Shoa (Chona) near Awash (Heonacha) River;[1] Takkaze [River]. *French Equatorial Africa:* Eguei. *Nigeria:* *Katsina Emirate. *Senegal:* Dagana; near Dakar; Saint Louis. *French West Africa:* Mauretania; Sudan and Niger Territories (*fide* Villiers *in litt.*).

Range. Trans-Africa from Eritrea west to Senegal in the vicinity of 15° N.

1 Mons. Paul Chabanaud informs us that Lefebvre left no map of his itinerary that would enable us to fix his localities with precision. Lefebvre's orthography, combined with some misprinting, renders the identification of his place names with currently recognized localities somewhat difficult. Thus "Chona", a misprint for Choua, = Choa or Shoa.

Erroneously reported from Antilles (Merrem); Buenos Aires (A. Duméril); Cape of Good Hope (A. Duméril); Giza, Egypt (Werner); Nyasaland (Johnston); Patagonia (Duméril and Bibron; Port Natal (A. Smith); South Afriea (Boulenger). The South American records are due to confusion with *Geochelone chilensis* (see Siebenrock:1912).

Geochelone pardalis babcocki (Loveridge)

1831c. *Testudo pardalis* Gray (part[1]), 12, pl. iii, fig. 3.
1835. Duméril and Bibron, 71.
1835. Temminck and Schlegel, 73.
1844. Gray, 7.
1851. Duméril and Duméril, 4.
1854a. Peters, 215.
1855. Gray, 9.
1862a. Strauch, 77.
1863b. Gray, 382.
1865. Strauch, 22.
1866b. Peters, 887.
1867a. Bocage, 217.
1869a. Peters, 11.
1870c. Gray, 6.
1872c. Gray, 4.
1873b. Gray, 5.
1878. Fisk, 790.
1878a. Peters, 202.
1880c. Vaillant, 8, 33, 88.
1882a. Peters, 2.
1884a. Rochebrune, 11 (but in error).
1886. Vaillant, 137.
1889. Boettger, 281.
1889a. Boulenger, 160.
1890. Strauch, 52.
1893a. Boettger, 9.
1893b. Boettger, 113, 122.
1893. Trimen, 79.
1894c. Günther, 85.
1895a. Bocage, 3.
1896a. Bocage, 97.
1896a. Boulenger, 546.

[1] Many of the following references might equally well be considered as "(part)" for they mention Bell's type, though their material is obviously *G. p. babcocki*.

1896c. Boulenger, 15.
1896. Tornier, 3.
1897g. Boulenger, 277.
1897. Johnston, 361.
1897. Meek, 184.
1897. Tornier, 63.
1898. Jeude, 3.
1898. Johnston, 361.
1898. Sclater, W. L., 96.
1898. Tornier, 282, fig. 1.
1899. Ansorge, 288.
1899a. Mocquard, 218.
1899. Siebenrock, 566, pl. iii, figs. 34-36.
1900. Peel, 333.
1900b. Tornier, 582.
1901. Lampe, 191.
1902d. Boulenger, 445.
1902. Scherer, 255.
1905. Neumann, 389.
1905c. Tornier, 366.
1906a. Duerden (not seen).
1906. Kammerer, 48.
1906a. Siebenrock, 823, fig. 3.
1907a. Boulenger, 6.
1907a. Duerden, 9.
1907. Lönnberg, 1.
1908. Chubb, 220.
1908a. Kammerer, 741, figs. 3-5.
1908b. Mocquard, 557.
1908. Werner (1907), 1826.
1909a. Chubb, 592.
1909b. Chubb, 34.
1909a. Siebenrock, 522.
1910. Siebenrock, 700, 716.
1910a. Werner, 300.
1911. Griffini, 3.
1911. Lampe, 146.
1911. Lönnberg, 7.
1911a. Masi, 29.
1911d. Sternfeld, 49.
1912b. Boulenger, 329.
1912c. Sternfeld, 198, 200.
1912b. Werner, 433.

1913c. Nieden, 54.
1913d. Werner, 40.
1914a. Hewitt, 244.
1915. Werner, 330.
1916. Calabresi, 42.
1919. Schmidt, 600.
1921d. Loveridge, 50.
1922. Falk, 163, fig. —.
1923g. Loveridge, 925, 931.
1924b. Loveridge, 2.
1925b. Flower, 925.
1927. Calabresi, 37.
1928. Cott, 952.
1928d. Loveridge, 49.
1929. Flower, 32.
1929h. Loveridge, 14.
1929. Rose, 188.
1931. Hewitt, 499.
1932b. Parker, 340.
1933h. Loveridge, 206.
1933a. Power, 214.
1934a. Mertens and Müller *in* Rust, 9.
1934. Pitman, 307.
1935b. FitzSimons, 303.
1937. Buxton, 101.
1937a. Flower, 9, 37.
1937b. Monard, 146.
1937. Ruckes, 103.
1939b. FitzSimons, 18.
1940a. Scortecci, 126.
1943. Scortecci, 270, 282.
1944. Leakey, 396, figs. —.
1946. Bally (1945), 163.
1946. Cairncross, 395, pl. i.
1946. Mitchell, 20.
1947. Stevenson-Hamilton, 319.
1950. Williams, 551, 552.
1952. Bally, 236.
1954. Battersby, 248
1954. Noël-Hume, 75, pls. i-iv.
1893a. *Homopus signatus* Boettger (part), 8 (juv. Shell ex Great Namaqualand).
1885. *Testudo sulcata* Smets (not of Miller: 1780), 8.

1904. *Testudo calcarata* Vaillant (part; not of Schneider), 186, figs. (are clearly of a juvenile *p. babcocki*).
1926. Tortoise, Bowker, 37.
1942. Hull, 125.
1948. Cooper, 11.
1933b. *Megachersine pardalis* Hewitt, 257.
1935c. *Testudo pardalis babcocki* Loveridge, Bull. Mus. Comp. Zool., 79, p. 4: Mount Debasien, Karamojo, Uganda.
1936h. Loveridge, 18.
1936j. Loveridge, 220, pl. i, figs. 1-2.
1937f. Loveridge, 492, 495.
1937d. Mertens, 2.
1947g. Loveridge, 136.
1949b. Loveridge, 19.
1953e. Loveridge, 158.
1955a. Mertens, 35, pl. iii, figs. 9-10; pl. xxii, figs. 129-134.
1955b. Mertens, 52.
1937a. *Geochelone pardalis* Hewitt, 789, pl. x, fig. 6.
1937e. Hewitt, 3 and G; pls. i, figs. 1, 3, 4; ivA, fig. 4; xxvii, fig. 4.
1948a. Archer, 74, figs.
1948b. Archer (part), 75, figs. (omit Keetmanshoop).
1950. Rose, 338, figs. 203-205.
1937b. *Testudo pardalis pardalis* Mertens (not of Bell), 5.
1955. Hellmich, 14, 15 (of reprint).

Common names. Eastern Leopard Tortoise; Mountain Tortoise. The first name, used by Gray (1855:9), is preferable, for the species occurs on the plains as well as on mountains, where it may be more frequently encountered today possibly as a result of its having been killed off on the lowlands. *Akuma*[1] (Karamojong); *anassi* (at Cape Delgado; Peters); *berg-schilpad* (Afrikaans: Bowker); *camba* (at Tete:Peters); *chepkoikochet* (Kipsigis and Nandi:Hull); *ekudu* (Samia:Hull); *ekutu* (Kitosh: Hull); *enkuru* (Kisii:Hull); *fulabomba* (at Capangombe:Bocage); *furgobi*[1] (Swahili); *ikudu*[1] (Gishu); *kamba*[1] (Nyungwe at Tete); *likudu*[1]: (Maragoli; Tereki); *lukutu* (Bunyore and Hanga:Hull); *malugangi*[1] (Gogo); *mfudi*[1] (Ganda); *nguru*[1] (Taita:Peters); *opuk* (Luo:Hull); *prokoch* (Suk:Hull).

[1] *Fide* Loveridge. Mitchell gives *furu* and *kamba* for tortoises but no evidence that *Geochelone* occurs at Dowa or Fort Maguire.

Description.[1] Beak scarcely to strongly hooked, edge of jaws strongly dentate; prefrontal large, frequently single but usually divided longitudinally; frontal broken up; remaining upper head

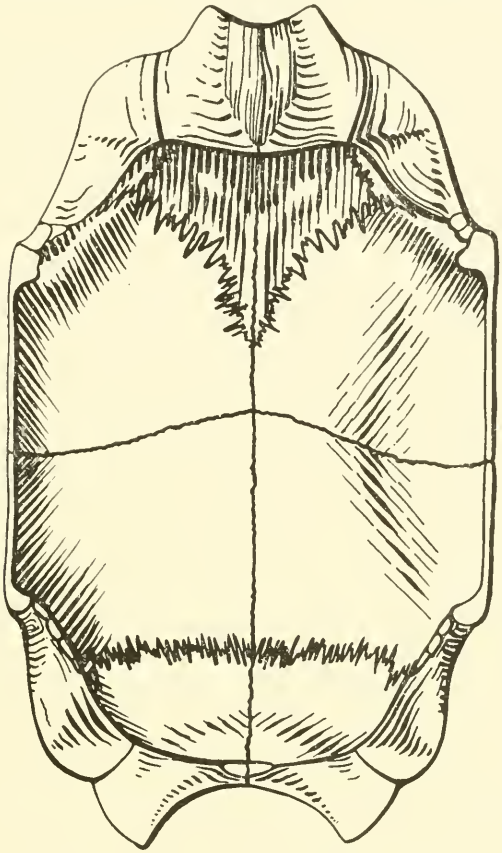


Fig. 18. Internal view of plastron of *Geochelone pardalis babcocki* (M.C.Z. 40004) (x ⅓).

(P. Washer del.)

shields small, irregular; forelimb anteriorly with large, unequal, usually scattered or rarely juxtaposed, generally imbricate

[1] Based entirely on material in the M.C.Z. unless otherwise stated.

scutes, forming 3-4 longitudinal and 7-9 transverse series from elbow to outer claw; claws 5; hinder side of thigh with 2 or more very large, rarely small, conical tubercles; heel with large, conical, spurlike tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace very convex, sides descending abruptly, deeply notched in nuchal region except in the very young, anterior margins not, and posterior margins only sometimes, expanded, reverted, and more or less strongly serrated; dorsal shields concentrically striated, sometimes swollen, subconical or convex; nuchal absent; vertebrals 5, rarely 6,[1] more or less convex, first as broad as, or broader than, long, the rest broader than long, broader than the costals; costals 4, rarely 5, not forming an angle with the marginals; marginals 10, 11 or 12;[2] supracaudal undivided, somewhat incurved.

Plastron with front lobe not or but slightly produced and not or but weakly notched; gulars paired; pectorals very narrow, their anterior border usually straight, widening abruptly towards the axillary notch; axillaries 2, one large, the other minute; inguinal moderate, normally in contact with the femoral, rarely separated;[3] hind lobe deeply or slightly notched posteriorly, usually angular, occasionally crescentic,[4] an interanal scute sometimes present.

Plastral formula: Abd > h > or = g > or < f > or = p > or < an.

Color. Carapace of hatchling[5] dull yellow, a broad black border (sometimes mottled with yellow) surrounds each vertebral and costal shield; within this border the ground color is light brown; typically each areola has a reddish brown border of moderate width within which there is *a single* central red-brown spot that usually coalesces posteriorly with the surrounding areolar border; upper and lateral edges of marginals and supracaudal bordered with black within which the areolae are edged with reddish brown. Plastral shields yellow, more or less mottled and edged with blackish brown. Head and limbs yellowish brown, uniform.

1 In a juvenile from Artu only, *fide* Tornier (1905c).
2 In a specimen (A.M.N.H. 50739) from Blanketi River, Tanganyika.
3 Separated only in a specimen mentioned by Hewitt (1931).
4 In the holotype ♀ (M.C.Z. 40003) for example.
5 Chiefly based on a series of specimens (M.C.Z. 42162-7) from Waterberg, Southwest Africa. For illustrations of juveniles from this area see Mertens (1955a:pl. xxii, figs. 129-134).

A juvenile from Ethiopia, referred to "*calcarata*" (=*sulcata*) by Vaillant (1904a) only differs from the Waterberg series in having lateral areolar spots alongside the central ones of the second and third vertebrals. Moreover Tornier (1905c:366) finds a 74 mm. "*pardalis*" (=*babcocki*) from "Artu," Ethiopia, differs but little from one taken in Hereroland, Southwest Africa. A Mongalla juvenile in the Vienna Museum, photographed for us by Dr. J. Eiselt, is very similar to these Ethiopian ones.

Two juveniles from the Ithanga Hills (M.C.Z. 31985) and Southern Guaso Nyiro (U.S.N.M. 41685), measuring 51 and 40 mm. respectively, have yellow carapaces whose shields are devoid of dark spots (except for an azygous spot on the fourth vertebral of the Guaso Nyiro tortoise). Both the dorsal and marginal shields of the latter have an inner dark border, while in the Ithanga Hills juvenile these borders are deep black and cover the sutures, coalescing with the corresponding borders of the adjacent shields.

Carapace of adults yellow with black markings. These are zonary in the young (whose areolae are usually brown) but radially arranged or broken in adults, where they may be so dense as to almost obscure the yellow ground color. Plastrons are invariably yellowish, either uniform or with black radiating streaks and scattered spots.

A Sudanese specimen in the British Museum, accompanied by full MS notes by Flower, is very light in color with very few black flecks. Another from the same locality is more nearly typical. According to Neumann (1905:389) Somali specimens are paler than those from Tanganyika, and Siebenrock (1906a: 823) suggests that tortoises from north of the equator tend to be lighter than those from the south, the coloring of young Sudanese *babcocki* approaching that of *sulcata*. Actually the carapace of a subadult Northern Guaso Nyiro specimen (M.C.Z. 7990) is heavily variegated with black except on the areolae.

The literature teems with descriptions of individual coloring. The pattern is discussed at some length by Duerden (1907b:74).

Size. Carapace length of a ♂ from Albany, 585 mm. (i.e. 23 inches in a straight line); 916 mm. (36 inches[1]) over the cara-

[1] Possibly it was these figures that gave rise to Stevenson-Hamilton's (1947: 319) misleading statement that leopard tortoises attain a maximum length of "between 2 and 3 feet" (i.e. about 609 to 914 mm.).

pace; girth 1116 mm. (44 inches) (Hewitt:1937e:4). Masi records (1911a:29) an unsexed Ethiopian specimen as 450 mm. Carapace length of a ♂ from Arusha, 340 mm., height 196 mm.; that of the holotype ♀ from Mount Debasien was only 364 mm., height 207 mm., being surpassed by a ♀ from Mount Mbololo with a length of 385 mm., and a height of 208 mm.

A table giving the length, breadth and height of twenty-three tortoises from Southwest Africa is given by Mertens (1955a:35). Length of claws on hind foot, 30 mm. (Cairncross:1946).

Weight. A ♀ from near Aberdeen, weighing about 18 lbs. when captured in 1929, has had its annual growth and fluctuating weight recorded by Cairncross (1946:395) from 3.vii.38 to 7.xii.41 when it attained about 500 mm. (19$\frac{9}{16}$ inches) in length, and weighed 45 lbs. Mrs. Leakey (1944:396) gives the weight of a ♂ as 18 lbs., and those of two ♀ ♀ as 37 and 45 lbs. respectively. Hewitt (1937c:4) mentions a ♂ of 50 lbs., while Archer (1948a:75) gives 69 lbs. as the maximum but states that some *babcocki* remain at about 10 lbs. while others continue to grow until they reach 30 lbs. Both the heaviest records appear to be those of specimens in the Albany Museum, Grahamstown.

Sexual dimorphism. While some individuals are readily sexed, others are not. Certain characters mentioned by FitzSimons (1985b:304), though doubtless satisfactory for his material, appear quite inadequate when applied to an extensive series. Thus there are exceptions to the general rule that the lower sides of the carapace are almost vertical in ♂ ♂ and bulging for the accommodation of eggs in adult ♀ ♀, though it remains a good average character. Again, the notch on the posterior lobe of the plastron is frequently more angular in ♂ ♂, though in one old ♂ there is scarcely any angle whatever, the sides being almost in a single plane; in the ♀ ♀ it is widely angular, even semicircular. The shape of the supracaudal, often thought to be diagnostic of sex, is not so in this species. The number of times the breadth of the carapace is contained in the length is largely an age character, ranging from 1.01 to 1.45 times in the young; 1.49 to 1.55 times in our 6 adult ♂ ♂; 1.45 to 1.68 times in the 10 oldest ♀ ♀. We are reduced to the following characters, therefore, of which the relative tail length is the surest guide.

Posterior third of plastron slightly concave in adults; tail long ..... ♂
Posterior third of plastron as flat as the rest in all ages; tail short ..... ♀

Breeding. When two ♂ ♂ and a ♀ shared an enclosure at the East London Museum, Archer (1948a:75) observed that the ♂ ♂ would push and butt one another until one of the combatants was overturned. Then, unless in a depression, the vanquished tortoise would right itself and hurry away. The victorious ♂ then pursued the ♀, which seemingly evinced no interest, bumping against her shell and walking around her — sometimes for hours at a stretch according to P. J. Styrdom (*in* Hewitt:1937e:6) — until pairing took place.

In East Africa, Bally (1952:236), who had a single ♂ confined with two ♀ ♀ (he has satisfied us as to sexing), states that it was the ♀ ♀ who butted each other's flanks until one of the contestants was overthrown. Furthermore, so Bally informs us (by mail), the larger ♀, apparently annoyed at the ♂ getting in her way, rammed him also! This seems to refute Hewitt's (1937e:6) statement that ♀ *pardalis* do not butt with the front of their shells.

Mrs. B. E. Leakey (1944:396) records that mating was a common occurrence among her captive tortoises. It began with the ♂ following one of the two ♀ ♀ around and around, occasionally for several hours, until he was accorded the opportunity to mount. On doing so he would extend his long neck and utter a husky cry that carried for a considerable distance. Hewitt (1937e:6) describes this call as "a peculiar grunting noise."

Nesting. For 2 or 3 days prior to laying, the expectant tortoise walks restlessly about the enclosure, pausing now and again to scratch the ground, while in each eye a frothy white foam[1] gradually accumulates (Cairncross:1946:395).

Apparently Duerden (1906a) was one of the first to record the nesting of this species, but a more detailed account is that given by Loveridge (1923g:926) of the nesting at Kilosa of a captive tortoise from Pwaga. Briefly it may be said that the reptile was first observed to be digging at 5.15 P.M. on May 21. Despite

[1] Probably an individual characteristic only.

the extreme hardness of the soil, a circular hole about 4 inches in diameter by 2 inches in depth had been dug already. Excavation was accomplished by the insertion of a hind foot which was scraped round and then brought up with a very small quantity of soil precariously balanced upon it; even so, at the last moment, much of the dirt fell back into the hole. The loss would have been even greater had not the tortoise from time to time micturated copiously so that the fluid, besides softening the hard ground, caked and bound the powdery soil. The hind feet were employed alternately with brief pauses for rest between the exchange. On reaching a depth of 4 inches the tortoise undercut the sides to form a gallery round the periphery, then continued excavating until a depth of 5 inches was reached.

Darkness fell at 6.30 P.M. At 7.12 P.M. the first egg was laid, its descent being retarded by an enveloping column of viscous fluid. At 7.24.10 P.M. the seventh and last egg was deposited. As each egg was laid the tortoise put down a foot and felt about for the egg which she then pushed beneath the undercut. At 7.26.10 P.M. the mother began breaking down the sides of the hole after which she proceeded to fill it in with all the recently excavated soil. Not once during the period of approximately three hours that she had expended on the task did the parent face about to examine the progress of her labours, or inspect the eggs which she had buried without ever seeing.

So impressed was Loveridge by the mechanical nature of the entire proceeding that he lifted the tortoise off the nesting site to some hard ground a couple of feet away. There she continued to trample without intermission until returned to the nest site. After a while she began raising herself on all four limbs as high as they would permit, then, suddenly relaxing, she dropped upon the site so that the disturbed soil was flattened by her plastron; this process of pounding the soil was continued for a long time. The following morning she was found to be resting on the site and, though the enclosure was a large one, she returned to sleep upon it that evening and for many subsequent nights. On June 12 Loveridge noted that not only did she sleep on the site but micturated and defecated on it frequently, if not daily. Other observers have reported that the

parent tortoise may be so exhausted by her efforts that she can scarcely drag herself away from the site.

Evidently nest holes vary considerably in size, for Archer's had a surface diameter of 6 inches and a depth of 8 inches. Cairncross says that his was 7 inches across at the surface, about 9 inches at the bottom, while the total depth was 9 inches. Mrs. Leakey's flask-shaped cavity was about a foot in depth, but had to accommodate an exceptionally large number of eggs, 30 in all. When numerous, the eggs are arranged in layers that are separated by earth (*fide* Bowker:1926). The number produced at one laying, therefore, ranges from 5 (Cairncross:1946:395) to 30 (Leakey:1944:396). Photographs of a nesthole being dug, and of one with eggs *in situ,* have been published by Cairncross (*loc. cit.,* pl. i), one of whose tortoises laid a total of 52 eggs (in 6 installments) during the summer of 1939-40. Their gross weight was 357.48 grams (about 6 lbs.).

Both in appearance and size the egg of a Leopard Tortoise rather resembles a pingpong ball but the porcelain-like shell is very brittle. Occasionally, as with poultry, a double, elongate egg with median constriction (figured by Archer) may be laid. Perhaps a tendency of this kind was exhibited by the Sudanese egg mentioned by Siebenrock (1906a:823) as measuring about 35 or 37 x 43 mm., unless the 43 was a misprint for 33 mm. Loveridge (1936j:220) removed 8 hard-shelled eggs measuring 36 x 38 mm. from a ♀ taken on Mt. Mbololo on April 17, therefore larger than the 7 measuring 32.5 x 35 mm. laid by a Pwaga tortoise on May 21, and smaller than 2, measuring 40 x 40 mm. and 38 x 40 mm., laid by a captive on August 5 and 25 respectively.

Eggs laid very early in the South African spring may hatch in 8 months provided that warm weather continues on into late autumn, but autumn laid clutches may take as much as 18 months to hatch if the following summer is cold (Archer:1948a: 75). Eggs laid in a Grahamstown garden on February 7, hatched on April 23 of the following year, i.e. they took 14 months, whereas two clutches laid in the South African autumn took only 11 and 12 months respectively (Bowker:1926:37). In South Africa, a presumably captive Leopard Tortoise laid 3

eggs on the ground at Grahamstown (Hewitt: 1937a:6), between July 26 and 28, mid-winter.

Mrs. Leakey (*in litt.*), after removing eggs from the nest, packed them in sand in a gasoline can which she placed on a cement hot-water tank. Nine months later, sometime between December 14 and 21, there emerged a single hatchling weighing half an ounce. As no others appeared during the succeeding 3 weeks the rest of the clutch were examined. Two eggs only held young tortoises, both of which were dead.

As eggs left *in situ* rarely hatched, Cairncross (1946:396) removed many clutches to an incubator where, except for a 10 minute cooling off period each morning, a temperature ranging from 88° to 92° was maintained for 6 months. The results were disappointing as the majority of eggs proved infertile. For further details consult his paper.

In one of Bowker's nests (1926:37) the central clay plug subsided slightly, permitting the hatchlings to squeeze their way out into the sunlight between plug and wall. Normally the young, whose shells are flexible at time of hatching, claw their own way to the surface. Being well supplied with nourishment from the yolk they require no food for several days, despite a display of considerable activity.

Growth. Rate of growth is affected by availability of food coupled with congenial temperatures, being accelerated during warm weather and retarded by cold. Good and bad seasons are reflected in the size of seasonal growth-rings on the shields of the carapace. In immature tortoises these rings furnish an indication of age, but becoming blurred with wear are no longer a trustworthy guide when maturity is reached. Consequently, statements regarding growth which are based on data derived from one or two tortoises, vary widely. P. J. Strydom is quoted by Hewitt (1937e:4) as saying that in South Africa only a few inches in length are gained during the first decade, making a total of 7 inches after 17 years. Archer's (1948a:75) detailed figures seem to support this. He furnished a growth chart of one of many tortoises (No. 64) studied at the East London Museum.

Fisk (1878:790) reports that two fully-grown "*pardalis*" were brought to Clanwilliam in 1846, and there remained without

progeny until 1857. In that year 2 young hatched from eggs laid by the ♀ and Fisk assumes this to imply that the parents had only then become adult! In 1877 the parents died within 3 months of each other, at which time, though 20 years old, the young ones were but two-thirds the size of their parents. The young were then deposited in the London Zoological Gardens.

Longevity. According to Flower (1937a:9) the record for known longevity is furnished by the above-mentioned tortoises which lived in captivity for over 30 years (1846-1877).

Diet. Principally grass, though they also feed on various succulents, crassulas, spekboom, thistles, prickly pear, pumpkins, beans and water melons (Hewitt:1937e:5); sweet potato tops or an entire, hard, white cabbage may be consumed at one meal (Leakey:1944:396); verdure of ground nuts, lettuce, and moistened bread (Loveridge:1933h:206); grapes (Rose:1950:339).

Bally (1946; 1952) observed a captive Ethiopian specimen take up and swallow a meatless chicken bone twice as long as its own head. Some days later the reptile was found nosing and pushing around a much larger bone. When Bally smashed this bone the tortoise seized the jagged splinters, one of which was an inch and a half long, and swallowed them one after another until all were gone. Thereafter he supplemented the reptile's vegetarian diet with a daily ration of bone splinters upon which it throve. For several years a companion tortoise from Lake Chala showed no interest in bones; then, in 1947, the Chala reptile also started eating chicken bones and doubled its weight in a year. It almost doubled its weight each succeeding year as the Ethiopian tortoise had been doing.

Bally tabulates the annual growth and his figures show that the Chala tortoise was still about doubling its weight each year in 1950, at which time the Ethiopian reptile's development was slowing down. Bally wondered whether the bone diet was responsible for the Ethiopian specimen's increase in size and weight during the years that the Chala tortoise remained almost static. (We reject the suggestion that Ethiopian tortoises possibly grow larger. There may be some confusion with *sulcata*.) A possible source of calcium for feral tortoises is to be found in the excrement of hyenas and other carnivores for captive specimens have been known to eat the dry dung of dogs as well as owl castings.

After eating, though it may have been on fleshy *Cissus* leaves or lettuce, Bally's tortoises drank regularly and eagerly. Though drinking copiously in summer, leopard tortoises can go for long periods without water (Hewitt:1937e:5).

Even when feeding daily on rich food a lapse of from 2 to 3 weeks occurred between defecations, Bally (1952:236) noted. The volume of such excrement was correspondingly large, frequently exceeding a tenth of the total weight of the depositor.

Parasites. Ticks (*Amblyomma exornatum* and *A. nuttalli,* not *A. marmoreum* as previously reported in error) were present on turtles from many localities.

Enemies. The eggs are dug up and devoured by dogs (Leakey), jackals, meerkats, muishonds. Young tortoises are attacked by crows and ground-hornbills, larger ones by ratels (Hewitt), seemingly by hyenas also; certainly by soldier ants (Loveridge). Nyamwezi tribesmen were seen eating them by Ansorge (1899: 288). Scherer (1902:255), when in the Mkomasi Valley, encountered a couple of Africans carrying a pair of poles to which was attached a huge tortoise about 500 mm. in length that the men said would provide them with a good meal. One of us (Loveridge) was told that in the Iringa Highlands a really large tortoise was considered to be worth 2 goats! According to FitzSimons (1935b:304) Bushmen prize these reptiles both for their flesh and shell. The latter, after removal of the plastron, is used for ladling or holding water, while Dr. R. Pöch states that the shields are made into snuffboxes by the Kalahari Bushmen.

At Magugu, Cooper (1948:11) found a tortoise, apparently of this species, lying on its back and unable to right itself. Surrounding spoor suggested that the reptile had been overturned by a buffalo's nose, after which the ungulate had pawed up the ground in the vicinity.

That many tortoises perish in the annual grass fires is suggested by Ansorge (1899:288) who not infrequently encountered their calcined remains. Many shells and skeletal remains, but no living tortoises, were found at Tsotsoroga by FitzSimons (1935b: 304) who concluded that the reptiles had perished during the extensive flooding of the flats a few years before.

Aestivation and Hibernation. In view of the admitted language difficulties, the alleged burying of this species during dry and cold seasons in Southwest Africa — as reported to Falk (1922:163) by Bushmen, should be received with reserve pending confirmation.

Migration. Peel (1900:333) reports seeing in Somaliland "a whole army of these monsters migrating" across the desert from one patch of grass to another.

Habitat. Leopard Tortoises inhabit the coastal plain and upland savanna, excluding areas of primary forest, in rather sandy, thornbush steppe and on kopjes. Such stone-strewn hills should have scattered scrub to provide shelter from the noonday sun. One tortoise, who skeleton was found between two sloping rocks by Loveridge, had presumably perished through inability to escape from its smooth-walled prison. The seeming predilection of this species for mountain masses (on Mt. Elgon it has been taken between 9,000 and 10,000 feet) may indicate that in such a habitat it is less liable to molestation from man and the larger carnivores. According to Kammerer (1908a:741) low temperatures are resisted better by Leopard Tortoises than by the giant Spurred Tortoise.

Localities. Sudan: Bahr el Ghazal Province (Werner:1924a); Bahr el Jebel (Gebel); Bor; Gondokoro; Lado Enclave; Mongalla; (the Omdurman market record of Kammerer is rejected). *Ethiopia:* Ado-Shebeli (Adoshebai) Valley; Araro (Arero); "Arruena" (?Arenda); Artu; Arussi Gallaland; Boorgha country; Caschei; Dabas (Daba-as); "Ennia Land" (? En); "Farre" (? Erre); Javello; Lake Abaya; Lake Zwai; "Lasman"; Neghelli; Shoa; Sibi; South of Harar (Harrar); "So-Omadu" (? Soddu). *British Somaliland:* Hargeisa; Nogal Valley; Toyo Plain (*ca.* 9°10′N.: 44°45′E.). *Somalia:* "Bambasse"[1] between Berdale (Bardale) and El Condul (Condut); Ircut (Pozzi-Ircudt); Jet; "Sahaieroi."[1] *Uganda:* *Mount Debasien. *Kenya Colony:* Athi Plains; *Guaso Nyiro; *Ithanga Hills; Kabete; Kaimosi; Kedong Valley; Kikuyu Escarpment south of Lake Naivasha; "Kipopotue, Ukamba"; Lekiundu River, Southern Guaso Nyiro; *Meru River Plains; "Mgana" (Betton coll. A locality unknown to L. Leakey and J. G. Wil-

[1] A Calabresi (1916) report on Stefani and Poli material; many misspellings.

liams); Mount Elgon; Mount Kenya; *Mount Mbololo; Mtito Andei; Murri; Nairobi; Ndi; Ndogo, Lake Baringo; Southern Guaso Nyiro; Turkana; *Wema, Tana River; *Ziwani Swamp, Northeast of Kilimanjaro (C.M.). *Tanganyika Territory:* *Arusha; Blanketi River; Busisi; Dodoma; Irazo; Kahama (Leiden Mus.); *Kilosa; Kondoa Irangi; Korogwe; Lake Eyasi; Lake Jipe; Lindi; Luguo; Magugu;[1] Masai Nyika and Steppe; Mbonoa; Mdjengo's; Mkaramo, near Mombo, Pangani River (1896); Mkomasi River; Moshi; Mtali's; Ruvu River, 33 km. s.e. of Moshi; Mwanza; Namanga; Ngare na Nyuki; Ngoma; Nzinga; *Pwaga; Ruwira; Sagayo; Sanga; *Saranda; Shinyanga; Simbo; *Singida; Tabora; Tambali; *Tukuyu; Ukerewe Id.; Ulugu; Usambara; Wembere; Zengeragusu. *Mozambique:* Cape Delgado Ids.; *Kasumbadedza; Sena; Tete. *Nyasaland:* (occurs south of the Mwanza River and west of the Shire in both Chikwawa and Port Herald districts, according to Mitchell: *in litt.*); Tengani. *Northern Rhodesia:* Luangwa (as Loangwa) River; Petauke. *Southern Rhodesia:* *Birchenough Bridge, Sabi River; near Gwamayaya River; Mount Darwin. *Bechuanaland Protectorate:* Gemsbok; Kalahari; Magalapsi; Makarikari; Maun; Serowe; Shaleshonto; Shorobe; Tsotsoroga Pan, Mababe Flats. *Transvaal:* Mannamead; Naauwpoort; Pietersburg. *Natal:* Durban. *Cape Province:*[1] Aberdeen; Albany; Alexandria district; Algoa Bay; Alice; Bathurst district; Brakkloof; Colesberg; Fort Beaufort district; Grahamstown; Hamburg; Hogsback; Keiskama; Malmesbury; Middleburg; Middleton; Modder River; Mortimer Road; Nonesis; Orange River Station; Port Elizabeth; Queenstown; Saint Clair; Somerset East district; Tarkastad; Tottabi near Alicedale; Uitenhage district; Vryburg; Warrenton; Willowmore. *Southwest Africa:* *Etosha Pan-near; Gibeon; Great Namaqualand; Karibib; Landsberg Farm, Luderitz district; Neudamm Farm; Ogosongomingo; Aus (Oas); Okahandja; Omaruru; Omatjenne; Rietmond near Gibeon; Swakopmund; *Tses (U.S.N.M.); *Waterberg; Windhoek (Windhuk).[2]

1 Unidentified "land tortoise" overturned by buffalo (Cooper:1948). Magugu, near Mbugwe, slightly south of Lake Manyara.

2 Through the courtesy of Mons. J. Guibé we have been able to examine one of Delalande's young tortoises from the "Cap." It is unfortunate that no more precise locality is known. In pattern it is a *p. pardalis* of the *"biguttata"* type, but in proportions is clearly referable to *p. babcocki* for its height of 45 mm. is included in its length of 83 mm., 1.84 times. It must therefore be considered an intermediate.

Angola: Benguela — inland from; Capangombe — some distance from; Cubal; Dombodola; Forte Rocadas; Mossamedes — interior of; Mupa.

Range. Sudan and Ethiopia south to Natal, west through Cape Province to Southwest Africa, where it meets with the typical form, but is dominant north of 27°S. and in southern Angola. It does not occur in northern Angola (*fide* Monard:1937b).

Erroneously reported from Madagascar (1873) and Senegambia (1884a).

Geochelone pardalis pardalis (Bell)

1828a. *Testudo Pardalis* Bell, Zool. Jour., **3**, p. 420, pl. xxv of Suppl.: "Promont. Bonae Spei," i.e. Cape of Good Hope.
1831b. Gray, 4.
1831c. Gray (part), 12 (omit figs. as these are of *p. babcocki*).
1835. Duméril and Bibron (part), 71 (color of young, etc.).
1836. Bell, text and col. pls.
1849. Smith, A., App., 1.
1851. Duméril and Duméril, 4.
1860. Fitzinger, 411.
1872b. Gray, 3, *in* Sowerby and Lear, pls. ix-x.
1892. ?Müller, F., 214.
1907b. Duerden, 74, fig., pl. vii, fig. 7 (showing juv. markings).
1829. *Testudo biguttata* Cuvier, Regné Animal, ed. 2, **2**, p. 10, footnote (*nomen nudum*): No locality.
1831c. *Testudo bipunctata* Gray, 12 (erroneously attributed to Cuvier mss. and cited with reference to the description of a juvenile in the Paris Museum).
1831b. Gray, 4 (erroneously attributed to Cuvier in Regné Animal).
1831c. *Testudo armata* Boie mss. Gray, 12 (listed as a synonym).
1831b. Gray, 4.
1835. *Geochelone pardalis* Fitzinger, 211.
1937e. Hewitt, pl. i, fig. 2; pl. ii, figs. 1-2.
1948b. Archer (part), p. 77 (Keetmanshoop specimen).
1935c. *Testudo pardalis pardalis* Loveridge, 4 (key).
1955a. Mertens, 35.

Most citations of "*pardalis,*" and one of "*pardalis pardalis,*" will be found listed under *p. babcocki,* with which race the typical form has been confused for almost a century.

Common names. Southwestern Leopard Tortoise (preferred); Mountain Tortoise.

Illustrations. Excellent colored plates of the ♀ holotype (side and plastral views) appeared in Bell's (1836) rare Monograph of the Testudinata, and were later reproduced by Sowerby and Lear (1872b). The distinctive coloration of the young *p. pardalis* has been figured by Duerden (1907b:fig. 7, based on a specimen beginning to assume the adult coloration), and by Hewitt (1937e:pl. 1, fig. 2, a hatchling closely resembling the Aroab specimen in the Museum of Comparative Zoology).

Description.[1] Beak moderately hooked, edge of jaws not strongly dentate; prefrontal large, divided longitudinally; remaining upper head shields small, irregular; forelimb anteriorly with a few large, unequal, widely separated, non-imbricate scutes, forming 3-4 longitudinal and 7 transverse series from elbow to outer claw; claws 5; hinder side of thigh with 2 large conical tubercles; heel with large, flat tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace flattened dorsally, sides nearly vertical (at least in ♂ adult), sloping gradually in young, deeply notched in nuchal region, in adults the anterior margin not, and lateroposterior margin only slightly, expanded and slightly serrated, its greatest height included more than twice (2.02 to 2.62 times) in its total length; dorsal shields concentrically striated except in young, their areolae slightly raised; nuchal absent; vertebrals 5, more or less (in young) convex, all broader than long, broader than the costals; costals 4, not forming an angle with the marginals; marginals 11; supracaudal undivided.

Front lobe of plastron anteriorly truncate in young, slightly produced and shallowly notched in adults; gulars paired; pectorals very narrow, their anterior border slanting in young, more or less straight, widening abruptly towards the axillary notch; axillaries 2, one small, the other minute; inguinal small, in contact with the femoral; hind lobe deeply notched posteriorly, almost crescentic.

Plastral formula: Abd>h>or=g>or<f>or=p>or<an.

Color. That of a hatchling from Aroab (M.C.Z. 22473) is strikingly different from juveniles of *G. p. babcocki*, viz. carapace dull yellow, black being confined to the narrow sulci surrounding

[1] Based on original description of ♀ holotype, the shell of an adult ♂ (M.C.Z. 16713) and an alcoholic juvenile (M.C.Z. 22473), together with notes on British Museum material as of 1953.

each vertebral and costal shield; these are edged with yellow, each areola with a reddish brown border, those on the vertebrals flanking a pale cream, broad, median band; upper and lateral edges of marginals and supracaudal bordered with reddish brown. Head and limbs peppered with black. The juvenile tortoise figured by Seba (1735:pl. lxxix:fig. 3), which Bell suggested might be the young of *pardalis,* is more probably a young *P. geometricus* of the *luteola* phase (see below).

The coloring of the adult, as described by Bell, is substantially similar to that of our specimen, also of the eastern race — *p. babcocki.* Carapace light yellow; shields with black, somewhat radiating, markings. Plastron dirty yellow, each shield with black spots, dashes, or radiating streaks extending inwards from the margins. Head, neck, feet and tail, dull brown with some admixture of dull yellow.

Size. Carapace length of type ♀, 432 mm., breadth 280 mm., height 213 mm.; carapace length of ♂ (M.C.Z. 16713), 302 mm., breadth 210 mm., height 147 mm.; carapace length of juv. (Aroab), 55 mm., breadth 42 mm., height 21 mm.

Enemies. Possibly the food value of this large tortoise may have led to its extermination on the Cape for today its range appears to be restricted to a small area in the southern part of Southwest Africa.

Habits. Bell (1828a; 421) states that since the beginning of summer the type had been living in his small orchard, feeding heartily on the grass which it plucked with movements similar to those "of a goose." The strength of an adult Leopard Tortoise is surprising for once it has braced its feet it is next to impossible to pull the reptile backwards. After its death, Bell (1836) dissected the type and found it held an estimated 200 ova ranging in size from those no larger than a pin's head to others equalling a pigeon's egg.

Localities. Cape Province: ? now extinct: Cape of Good Hope [1] (Type); Olifants River (Delalande coll. ? this subspe-

[1] Walter Rose informs us (6.v.54) that, during thirty years of rambling in the vicinity of Cape Town, he has never encountered a leopard tortoise — except escapees. He believes it formerly occurred 45 miles northwest of Cape Town in the Malmesbury district where one meets with arid conditions resembling those of the Karroo.

cies). *Southwest Africa:* *Aroab; Keetmanshoop[1] *Kolmanskop;[2] Rehoboth.[3]

Range. Southwest Africa possibly as far north as Rehoboth,[3] more certainly south of a line from Kolmanskop (near Luderitz Bay) to Keetmanshoop, south (in former times presumably) to the Cape.

Erroneously reported from Angola (Monard: 1937b).

Genus TESTUDO Linnæus

1758. *Testudo* Linnaeus, Syst. Nat., ed. 10, 1. p. 197. Type: *Testudo graeca* Linnaeus (designation by Fitzinger).

1820. *Chersine* Merrem, Vers. Syst. Amphib., pp. 12, 29. Type: *T. graeca* Linnaeus (designation by Lindholm).

1830. *Chersus* Wagler, Natur. Syst. Amphib., p. 138. Type: *Testudo marginata* Schoepff (by monotypy).

1869e. *Peltastes* Gray (not of Rossi: 1807), Proc. Zool. Soc. London, pp. 167, 171. Type: *T. graeca* Linnaeus (designation by Lindholm).

1870e. *Chersinella* Gray, Suppl. Cat. Shield Rept. Brit. Mus., part 1, p. 8. Type: *T. graeca* Linnaeus (designation by Lindholm).

1870e. *Testudinella* Gray (not of Bory: 1826), Suppl. Cat. Shield Rept. Brit. Mus., part. 1, p. 12. Type: *T. horsfieldi* Gray (by monotypy).

1872e. *Peltonia* Gray, App. Cat. Shield Rept. Brit. Mus., part 1, p. 4. Nom. nov. for *Peltastes* Gray (preoccupied).

1916. *Medaestia* Wussow, Wochenschr. Aquar.-Terrar. Kunde, 13, p. 170. Type: *T. graeca* Linnaeus (designation by Mertens).

Definition. Skull with triturating surface of maxilla moderately or weakly ridged or without ridging; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina small, concealed or large and conspicuous; *prootic typically concealed dorsally and anteriorly by parietal;* quadrate enclosing stapes or not; surangular subequal in height to prearticular; neck with third or fourth centrum biconvex.

[1] This Keetmanshoop record is assumed solely on geographical grounds, being taken from Archer (1948b:77) who lists it with many others as *Geochelone pardalis.*

[2] It is only right to mention that in the Vienna Museum there is a specimen allegedly from Swakopmund (Poch coll.) whose breadth is contained in its length 2.10 times, and another of 2.11 times from Aus where Poch collected many *G. p. babcocki.* We propose regarding these two individuals as intermediates between the two races which meet in the Luderitz Bay region.

[3] The Rehoboth record is based on a photograph of two young specimens kindly sent to us by Dr. Robert Mertens in a letter of 18.v.56.

Carapace never hinged; typically the anterior neurals alternately octagonal and quadrilateral; outer side of third costal scute about as long as, or longer than, that of fourth; submarginal scute absent; frequently a single suprapygal, if two, they are typically separated by a straight transverse suture.

Plastron with posterior lobe more or less hinged in one or both sexes; gular region but little thickened or produced; gulars paired, longer than broad.

Range. Northern Africa, southern Europe, and western Asia.

Fossil record. Extensively known from the Cenozoic of Europe, and since the Pliocene from North Africa.

Remarks. The genus *Testudo* includes forms of moderate to small size, the living species attaining as much as 280 mm. in some cases, as little as 120 mm. in one instance.

Testudo graeca, though technically the type of *Testudo*, is not typical of the Boulengerian grouping which has gone under this generic name. In our belief, as indicated in the diagram of relationships above (Fig. 8), *Testudo graeca* and its immediate relatives are not closer to the species *pardalis* or *elegans* or *denticulata* or *gigantea* or *emys* or *radiata* than are the species of *Gopherus* or of *Homopus*, forms which have long been put in distinct genera. Though conventionally the *graeca* group, at best, has been one subgenus among many subgenera, an inspection of the characters by which the subgenera that we unite under *Geochelone* are separated, and a comparison of these with the peculiarities of the *graeca* group, makes it plain that different orders of magnitude of divergence are involved.

We have here suggested the separation of two larger genera *Geochelone* and *Testudo* — as well as the smaller units *Malacochersus, Psammobates* and also *Chersina*, the latter all Ethiopian endemics. We have considered another possibility, that, while the Ethiopian endemics might still be separated, *Geochelone* and *Testudo* might be regarded as subgenera within a larger concept of *Testudo*. This would have the apparent merit of removing from the Boulengerian genus *Testudo* only the Ethiopian forms that have never fulfilled the Boulengerian definition of the genus But it appears to us that this suggestion founders when the *Gopherus-Stylemys* lineage is taken into account. The *Gopherus-Stylemys* line has quite as much in common character-

wise with *Testudo* and *Geochelone* as these have with each other. Recent *Gopherus* has the maxillary ridging, the concealed anterior palatine foramina and the octagonal and quadrilateral neurals that occur, though not quite invariably, in the other two groupings. The *sole* conspicuous distinction is the median premaxillary ridge, seemingly a triviality. Considering only Recent material, as Boulenger did, it was entirely logical for him to include *Gopherus* in *Testudo*.

But the evidence now available from the fossil genus †*Stylemys*, which has the gopheride premaxillary ridge and is clearly a close cousin of *Gopherus*, transforms the entire picture and reveals that the roots of the gopheride lineage go back to forms with many emydine characters. Thus it has been demonstrated (Case 1936 [1]; Williams:1952) that the North American Oligocene species †*Stylemys nebrascensis* had neurals with the primitive emydine shape (hexagonal, short sided in front), and in both fore- and hind feet the emydine phalangeal formula of 2,3,3,3,3.

Thus it is necessary to face the fact that *many of the characters common to modern land tortoises*—for example, *Geochelone, Testudo, Gopherus* and *Pyxis* share the octagonal and quadrilateral neural pattern — *have been acquired in parallel.* Formerly this fact so impressed one of us (Williams:1950; 1952) that *he questioned the naturalness of the subfamily Testudininae.* Further investigation and consideration has convinced him that all the land tortoises do spring from a common root within the Emydinae. He now believes that the major lines within the land tortoises had their start in the beginning of the Tertiary with an ancestral form that in terms of its characters was then only a slightly divergent emydine and only prospectively a testudinine. It appears to him that as a correlative of this view, it is desirable to recognize at least one genus for each of the major lineages that go back to the postulated ancestral testudinine.

It is on the basis of this interpretation that we venture to break up the Boulengerian genus *Testudo* and restrict its concept to the *graeca* group. Previously (p. 218), we have mentioned two distinctive characters of this genus — the posterior plastral hinge (present in one or both sexes), and the concealed prootic. A third, heretofore neglected, character which we have found

[1] Case, E. C., 1936, Contrib. Mus. Paleont. Univ. Michigan, 5, pp. 69-73.

useful enough to employ in the key (p. 221), is the presence of distinct supranasal scales (Fig. 19) otherwise occurring only in *Malacochersus*. Perhaps this implies affinity between these two genera. However, we are inclined to believe that a rather elabor-

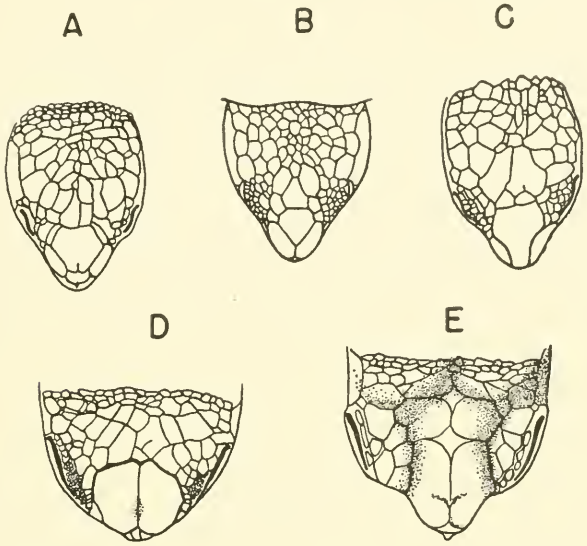


Fig. 19. Head scalation in certain testudinines (cf. Fig. 22). *A, Testudo hermanni* juv. (M.C.Z. 3063); *B, Malacochersus tornieri* (after Procter: 1922b); *C, Testudo g. graeca* juv. (M.C.Z. 1497); *D, Geochelone p. babcocki* juv. (M.C.Z. 40005); *E, Kinixys erosa* juv. (M.C.Z. 12583).
(P. Washer del.)

ate head squamation was primitive for tortoises, and that breakdown of this condition has occurred to a greater or lesser extent in many lines. In any event, and in spite of a certain amount of variation (Fig. 22), this character proves a valuable external indicator for the genus.

Within the restricted genus *Testudo* there are groupings at various levels. We recognize two subgenera, both African, which may be defined as follows:

Key to the Subgenera of TESTUDO

Maxillary with weak to moderate ridges; quadrate enclosing stapes. Range: Northwest Africa; southern Europe; western Asia .....
Testudo Linnaeus (p. 261)

Maxillary without ridges; quadrate not enclosing stapes. Range: Northeast Africa (Tripoli and Egypt only) .....
Pseudotestudo new subgenus (p. 276)

The subgenus *Testudo sensu stricto* is here interpreted to include only *graeca, marginata, horsfieldi* and *hermanni.* Of these *hermanni* appears to be the most primitive, possibly the most primitive in the entire genus. Both its external and internal characters testify to this. Externally the forelimb has relatively small and numerous scales (in as many as ten longitudinal rows) the larger ones mostly toward the outer side, and the supracaudal is divided. The presence of a tail claw may also be primitive for the genus. Internally the skull shows relatively strong ridging on the maxilla and the anterior palatine foramina are fully concealed. The trachea (*fide* Siebenrock) is unspecialized in not being excessively long and coiled as in the two other members of the subgenus in which this character has been studied. In all these respects *graeca* is more specialized than *hermanni;* while *marginata,* as Siebenrock (1910) has shown, is extremely close to *graeca.* The two form a transition to the very specialized dwarf species *kleinmanni, graeca* in particular being close enough to suggest that *kleinmanni* was ultimately derived from it.

Testudo graeca has the scales of the forelimb enlarged and forming 4 to 6 longitudinal rows, a trend continued by *kleinmanni* in which there are usually only 3 in longitudinal series. In both *graeca* and *kleinmanni* the supracaudal is usually single, and the tail claw is rudimentary or absent in both species. As compared with *hermanni* the maxillary ridging is reduced in *graeca,* absent in *kleinmanni.* The anterior palatine foramina, more exposed in *graeca* than in *hermanni,* are fully exposed in *kleinmanni.* In possessing a long and coiled trachea, *graeca* is more specialized than *kleinmanni;* however, it is in the *largest* individuals of *graeca* and *marginata* that this condition is most pronounced (Siebenrock:1910). In one respect *kleinmanni* differs from other members of *Testudo* in a way not approached by *graeca,* i.e., in having the quadrate open behind, not enclosing

the stapes. In size the two species differ radically, *graeca* being one of the largest members of the genus and *kleinmanni* decidedly the smallest. However, this disparity is bridged by an allegedly dwarf subspecies, if valid, *T. graeca floweri* of southern Palestine (cf. Flower :1933 :745).

Testudo kleinmanni, despite the numerous ways in which it is approached by *graeca,* from which in all probability it is directly derived, is still a species rather sharply set apart. It might be said to represent only the extreme of trends within *graeca,* but the differences are abrupt and very striking. The end result is a species which, in many of the characters considered of taxonomic value by Boulenger (and for the most part so considered by us), parallels forms that are almost certainly not closely related. In the absence of maxillary ridges it parallels *Pyxis, Psammobates, Chersina, Homopus* and *Kinixys,* and parallels as well the last two in its fully exposed anterior palatine foramina. In the quadrate failing to enclose the stapes it displays an emydine character (probably secondary) elsewhere found in testudinines only in *Pyxis arachnoides,*[1] and *Geochelone sumeiri* (type specimen examined at the Tring Museum).

If as we suspect it is a derivation of *graeca, Testudo kleinmanni* must surely have been at one time only a geographical form of *graeca.* It is still allopatric to that species, dividing the present range of *graeca* in two. This singular fact of distribution is indeed our only clue, for in Africa there is no fossil evidence on which to found an opinion on the circumstances of *kleinmanni's* origin, and the evidence from Europe has not been sufficiently analyzed.

Testudo graeca of North Africa and southern Spain is probably racially distinguishable from the populations of eastern Europe and Asia. However, Mertens (1946d) who separated it as *g. graeca,* found only minor differences in shell proportions between the typical form from North Africa and his *g. ibera* ranging from the Balkans to Persia. Certainly the populations of eastern Europe and Syria do not differ greatly from those in Africa. If one may deduce from this that the separation of the African and east European races has not been of long standing, it is natural

[1] In *Pyxis* the condition is quite different and not primitive. The skull structure of this genus and of *Acinixys* is to be described in a separate paper by one of us (E.E.W.).

to infer that formerly a continuous population extended across southern Europe whence the invasion of western North Africa occurred via Spain and *not* across Egypt. In this view the southern Spanish population of *g. graeca* would be a relict one, persisting after the general extinction of the species in western Europe. This might be due to an invasion by *hermanni* which now occupies much of the region separating the two ranges of *graeca* in southern Europe.

If this hypothesis is correct, then *Testudo kleinmanni* is not a peculiar form that has differentiated in the middle of the geographic range of its parent species. Instead, at the time of its origin, it was the most westerly form of the *graeca* complex on whose periphery it developed. If in southern Palestine there is really a dwarf race (*T. g. floweri* Bodenheimer: 1935[1]) resembling *kleinmanni* in coloration — and a single shell [2] in the British Museum seems to support this view — the case for our hypothesis respecting the mode of origin of *kleinmanni* will be strengthened.

Key to the Circum-Mediterranean Species of TESTUDO

1. Forelimb anteriorly with 7-10 small scales across it; hinder side of thigh without enlarged tubercle; tail terminating in a distinct claw, always present; supracaudal usually divided. Range: southern Europe[3] ..... *hermanni* Schneider

   Forelimb anteriorly with 3-6 larger scales across it; hinder side of thigh with or without a large tubercle; tail claw present or absent in all three species; supracaudal usually undivided 2

2. Forelimb anteriorly with 3-6 scales across it; hinder side of thigh with a large tubercle. Range: western North Africa and southern Spain (with races in extreme southeastern Europe and western Asia) ..... *g. graeca* Linnaeus (p. 261)

   Forelimb anteriorly with 3-5 scales across it; hinder side of thigh without enlarged tubercle 3

[1] Bodenheimer, F. S., 1935, "Animal Life in Palestine" (*fide* Mertens: 1946d). We have also found the name referred to in Mém. Inst. Egypt, 1937, **33**, p. 71.

[2] While the carapace of this specimen (examined by us) has the predominantly yellow hue of *kleinmanni*, the plastron was much blacker than in that species; also the pectoral shields were larger than the femorals, the reverse of the *kleinmanni* condition. While having the appearance of an adult, the length of its carapace is only 114 mm., that of its plastron 97 mm.

[3] As Lortet (1887:6) distinctly states that he never collected this species in Syria, the specimen from Antakia, Syria, allegedly collected by Lortet, and recorded as "*graeca*," i.e. *hermanni* by Boulenger (1889a:177) requires confirmation.

3. Forelimb anteriorly with 5, rarely 4, scales across it; supracaudal and posterior marginals spread out; coloration predominantly black; size moderately large, maximum length of carapace about 280 mm. Range: Greece only ..... *marginata* Schoepff

   Forelimb anteriorly with 3, rarely 4, scales across it; supracaudal only spread out; coloration predominantly yellow; size small, maximum length of carapace not exceeding 127 mm. Range: eastern North Africa (Tripoli and Egypt) .....*kleinmanni* Lortet (p. 276)

Subgenus TESTUDO Linnæus

1835. *Testudo* Fitzinger, Ann. Wiener Mus., **1**, pp. 108, 113, 122: Type species: *Testudo graeca* Linnaeus.

Definition. Supracaudal divided or single. Maxillary weakly to moderately ridged; anterior palatine foramina at least partly concealed in ventral view; quadrate enclosing stapes. Plastron of adults with a more or less movable posterior lobe in one or both sexes. Tail claw present or absent.

Range. Northern Africa, southern Europe, western Asia.

TESTUDO GRAECA GRAECA Linnaeus

1758. *Testudo graeca* Linnaeus, Syst. Nat., ed. 10, **1**, p. 198: Africa.
1774. Müller, S., 44.
1789. Poiret, 358.
1804. Blumenbach, 66 (illus. no.).
1828. Bory de St. Vincent (part), 73.
1833. Rozet, 232.
1835. Temminck and Schlegel (part), 70.
1860. Tristram, 405.
1867a. Steindachner, 4.
1872b. Gray, 4, *in* Sowerby and Lear, pl. xvi (but omit "Asia Minor").
1880c. Vaillant, 8, 33, 88, pls. xxv; xxvii, fig. 5.
1886. Eade, 316.
1893. Eade, 368.
1924a. Flower, 921.
1925. Flower, 929.
1926. Flower, 133.
1929. Flower, 28.
1932. ?Thomson, 362, pls. —.

1933. Flower, 744.
1934a. Mertens and Müller *in* Rust, 9 .
1936b. Mertens, 15, figs. 2-3.
1937a. Flower, 6-9, 36.
1937. Hediger, 187, 191.
1946d. Mertens, 112.
1948. Astré, 60.
1949. Moyle, 582.
1950. Williams, 550.
1951. Aellen, 167, 195.
1952. Williams, 555, 556.
1954. Noël-Hume, 20, figs. 5-6.
1766. *Testudo pusilla* Linnaeus (part: not of 1758), 353.
1802. Shaw (not of Linnaeus: 1758), 53.
1862a. Strauch, 67.
1862b. Strauch, 14.
1865. Strauch, 14.
1874. Boettger, 123.
1880c. Vaillant, 8, 26, 88.
1886. Vaillant, 135.
1890. Strauch, 45 (but omit Asiatic localities).
1898. Jeude, 2.
1835. *Testudo Mauritanica* Duméril and Bibron (part), Erpèt. Gén., 2. p. 44: Mauritanica; Algeria (omit coasts of Caspian Sea, etc.).
1850. Guichenot, 1.
1854. Eversmann, 443.
1857. Jan, 35.
1875. Kercado, p. xxxv (*Tistudo Mauritonica*).
1894. Oliver, 102.
1896b. Oliver, 118.
1897. Bateman, 48.
1904. Chaignon, 2.
1905. Barbier, 78, pl. iii.
1907. Le Cerf, 22.
1912. Kollman, 103 footnote.
1919. Leblanc, 178, figs. 1, 5, 6.
1920. Mourgue, 233.
1836. *Testudo marginata* Gervais (not of Schoepff), 309.
1841. Schlegel, 138.
1848. Gervais, 204.
1884a. Rochebrune (erroneous report of occurrence in Senegambia) 15.
1898. Jeude (erroneous listing of skeletal material from Cape) 2.
1836. *Testudo ibera* Gervais (not of Pallas), 309.

1848. Gervais, 204.
1851-64. Blanchard, 72, pls. i-ii (skull, carapace, etc.).
1851. Eichwald, 414.
1877. Camerano, 97, pl. iv.
1883a. Boettger, 130.
1885b. Boettger, 472.
1887. Lortet (part), 3, pl. i.
1889a. Boulenger, 176.
1891c. Boulenger, 96, 104.
1892. Anderson, 11.
1892. Koenig, 15.
1892a. Werner, 354.
1892b. Werner, 269.
1893a. Boettger, 11.
1894. Werner, 75.
1895. Koenig, 403.
1895c. Werner, 127.
1896. Anderson, 111.
1896. Escherich, 278.
1899. Doumergue, 243.
1900. Boettger and Tornier, 64.
1901. Gadow, 369.
1901. Lampe, 193.
1903. Mayet, 10.
1906c. Siebenrock, 847.
1908. Kerville, 96.
1908. Zulueta, 451.
1909a. Siebenrock, 540.
1909a. Werner, 597, 628.
1911. Lampe, 147.
1912a. Pellegrin, 256.
1912b. Werner, 448.
1913. Ghigi, 266, 283.
1913b. Siebenrock (part), 24, figs. 10-19.
1919. Leblanc, 177.
1922b. Procter, 493, figs. 1a, 11b.
1922. Zavattari, 15.
1923a. Calabresi, 7.
1924a. Flower, 920.
1924. Zavattari, 15.
1926a. Pellegrin (1925), 315.
1927a. Pellegrin, 261.
1928. Hediger, 408.

1929. Lindholm, 295.
1929b. Werner, 15, 21.
1929. Zavattari, 86.
1930a. Zavattari, 263.
1931c. Werner, 275.
1932. Thomson, 363, pls. —.
1935. Hediger, 3.
1935. Laurent, P., 345.
1937. Zavattari, 530.
1944b. Kehl, 166.
1948. Astré, 60.
1953. Burton, 34, fig., photo.
1836. *Testudo Whitei* Bennett, in White, Nat. Hist. Selborne, p. 361, fig.: No locality given, but type in British Museum.
1841. *Testudo graeca* var. *mauritanica* Schlegel, 106.
1857. *tortue terrestre* Labouysse, 86.
1870e. *Peltastes marginatus* var. *whitei* Gray, 11.
1873c. *Chersinella graeca* Gray, 725, pl. lx, fig. 4 (skull: African).
1880d. *Testudo campanulata* Peters (not of Strauch)[1], 305.
1881a. Peters, 365.
1928. *tortue d'Algerie* Bailly-Maitre, 111.
1946d. *Testudo graeca graeca* Mertens, 112.

Further citations of "*graeca*," "*mauritanicus*," "*marginata*," and "*campanulata*," will be found under *Testudo kleinmanni*. Owing to the composite and frequently involved nature of many of the early references to "*graeca*," we have preferred to omit them unless they definitely mentioned a North African locality.

Synonymy. The name *graeca* (according to Statius Müller: 1774, as quoted by Siebenrock:1913:26) was given to this tortoise by Linnaeus on account of its carapacial pattern resembling Grecian mosaic work. It was entirely without reference to its place of origin which Linnaeus quite definitely stated to be Africa, after Edwards (*circa* 1743-8: Nat. Hist. Birds, part iv). In this work the life-sized colored plate carries this caption:

[1] Strauch (1862b, Mem. Acad. Imp. Sci. St.-Pétersbourg, (7), **4**, No. 7, p. 14) lists *campanulata* as occurring in Algeria though not seen by him. His description is of *marginata*. Strauch attributes the authorship of *campanulata* to Walbaum (1782, Chelonogr. Beschr. Schildkröten, pp. 80, 124), but Walbaum's name — "*Lorica varietatis tabulatae testudinis campanulata*" — is not binomial and consequently invalid; furthermore, it apparently does not refer to an African species.

"No. 204. The African Land-Tortoise.
Loc. Santa Cruz in West Barbary."

i.e., the old Spanish fort of Santa Cruz near Oran, Algeria (*fide* Strauch:1862a), and the reptile figured is quite identifiable.

Strauch (1862a:67) points out that *graeca* Linnaeus, 1758, and *pusilla* Linnaeus, 1758, are not specifically the same, the latter being a composite; but *pusilla* Linnaeus (in part), 1766, and *pusilla* Shaw, 1802, were both based on Edward's specimen and are consequently synonymous with *graeca* Linnaeus, 1758.

The first to point out that *graeca* was the correct name to apply to the African species, was Siebenrock (1913, Ann. k.k. Naturhist. Hofmus. Wien., 196-197) but because *ibera* Pallas 1831 had long been employed for this species, he preferred to continue use of the latter name. Subsequently Flower (1925b; 929) pointed out that the type of *ibera* came from Iberia in Transcaucasia (cf. Pallas, 1811, Zoogeographia Rosso-Asiatica, **3**, p. 18, pl. ii, figs. 2-3). Specimens (M.C.Z. 5301-2) from Tiflis, Transcaucasia, suggest that this is a race of *graeca*, recognizable by its broad and low-vaulted carapace. *T. g. ibera* has been considered by Mertens (1946d:112) as one of several races inhabiting Asia Minor, their range separated from that of *T. g. graeca* by Egypt.

Testudo graeca bettai Lataste, based on an old specimen of unknown origin, having a divided supracaudal and a caudal spur, but lacking a conical tubercle on the hinder side of the thigh, appears to be a straight synonym of *hermanni* Gmelin, 1789, except for its allegedly 4-clawed forefeet and 3-clawed hind feet.

Common names. Western Spur-thighed Tortoise (preferred); Mosaic Tortoise (Müller:1774); Moorish Tortoise (Bateman: 1897); Spur-thighed Mediterranean Land-Tortoise (Flower: 1925); *Fakroun* (Tunisian Arabic: Mosauer); *makroona* (Algerian Arabic:Koenig); *zolhafie* (Arabic:Forskål).

Illustrations. The finest colored representations of this tortoise are those to be found on plate xvi of Sowerby and Lear (1872b), correctly labeled *graeca;* and on plate i of Lortet (1887) where it is miscalled *ibera.*

Description. Beak weakly hooked, tricuspid; edge of jaws not dentate; supranasals present, not meeting medially; prefrontal entire, rarely divided longitudinally;[1] frontal large,

[1] Occasionally divided longitudinally in *"ibera"* according to Boulenger (1889a).

occasionally broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with large to very large, unequal, juxtaposed, more or less imbricate, rounded (young) to pointed (adult) scutes forming 3-6[1] longitudinal and 4-7 transverse series from elbow to outer claw; claws 5;[2] hinder side of thigh with a very large flat or subconical tubercle; heel with or without an indefinite spurlike tubercle; claws 4; tail without, or with a poorly developed terminal clawlike tubercle.

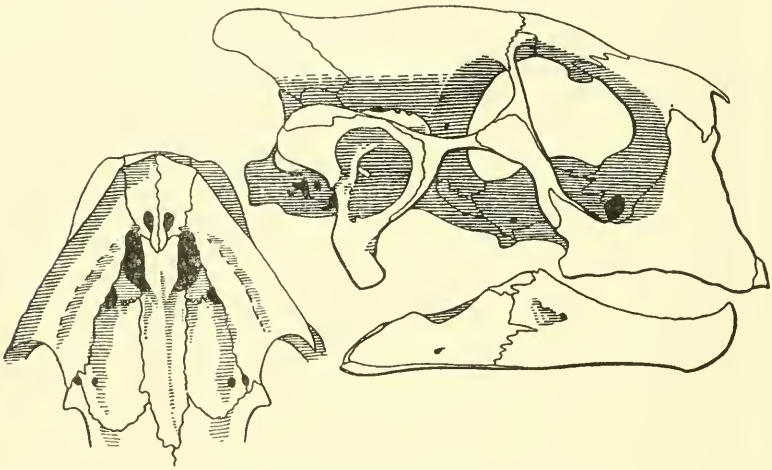


Fig. 20. Skull of *Testudo graeca graeca* (M.C.Z. 4485). Condylobasal length 26 mm.

(S. McDowell del.)

Carapace convex, slightly depressed in young only, sides descending abruptly, broadly notched in nuchal region, anterior and posterior margins not expanded, not or but slightly reverted, not or but slightly serrated; dorsal shields concentrically striated, not or but slightly swollen; nuchal moderately elongate, often broader behind, rarely divided longitudinally;[3] vertebrals

[1] Three on left, four on right of an Algerian specimen (M.C.Z. 4485).

[2] Flower remarks (1924:921) that of 31 tortoises of unknown parentage (though presumably of Mediterranean origin) hatched in Giza Zoological Gardens between the years 1907-192 , 12 had 4 claws on their forefeet, 7 others bore 5 claws, and the condition in the remaining 12 was not noted.

[3] Divided in a North African tortoise (Lampe:1901).

5, rarely 6,[1] the first as broad as or broader than long,[2] second to fifth narrower or broader than the costals; costals 4, rarely 7 or 8,[1] not forming an angle with the marginals; marginals 11, rarely 10; supracaudal undivided, rarely divided;[3] not projecting beyond the marginals, slightly incurved in ♂ ♂, occasionally in ♀ ♀.

Front lobe of plastron anteriorly truncate, not or but slightly

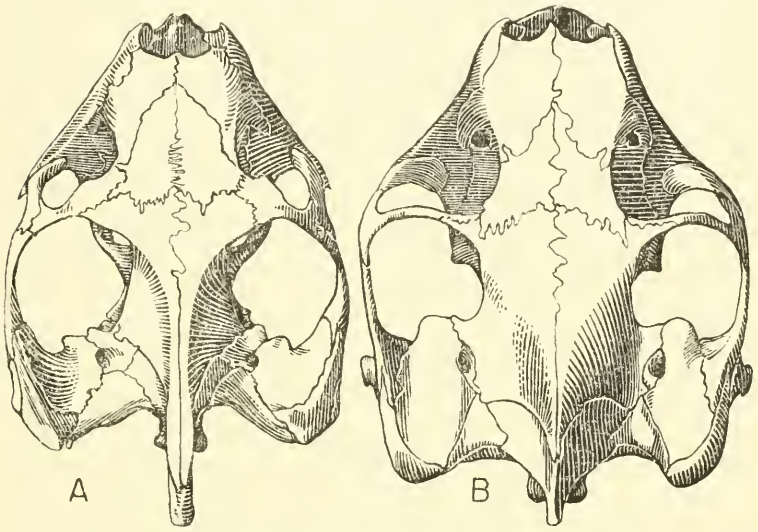


Fig. 21. Typical condition of prootic in dorsal view of skulls. *A*, *Geochelone p. babcocki* (A.M.N.H. 7203) showing prootic exposed; *B*, *Testudo g. graeca* (M.C.Z. 4485) showing prootic concealed.

produced and not or but slightly notched; gulars paired; pectorals moderate, their anterior border usually curved and widening towards the axillary notch; axillary 1, small or moderate; inguinals (apart from some accessory scales) 2, outer moderate.

[1] Six in an abnormal living individual which had 7 costals on the right and 8 on the left (Mertens: 1936b: figs. 1-2).

[2] The third vertebral was always broader than or equal to the fifth in young Giza-bred tortoises, in older ones the third was narrower than the fifth (Flower: 1924a).

[3] Occasionally divided in young (*fide* Koenig: 1892) or adults (Doumergue: 1899).

triangular, inner small, quadrate and in contact with the femoral; hind lobe broadly notched posteriorly, especially so in ♂♂, immovable in juveniles[1] but in life more or less movable in adults of both sexes.[2]

Plastral formula: Abd>(g. h. p. f. an: very variable).

Color. Carapace of young yellowish or pale olive, each shield bordered with black and brown and usually bearing a central black spot.

In adults yellowish, pale olive, brownish to reddish brown, rarely uniform; the darker pattern as described for the young but much more irregular with black predominating. Plastron usually yellow or greenish yellow, occasionally light brown, most or all of the shields bearing a blackish blotch. In ♂♂, according to Doumergue (1899), the plastron has a tendency to be more melanistic than in the ♀♀.

Size. Carapace length of a ♂ (M.C.Z. 18161) from Bone (which lived for over twenty years — 10.vii.1890 to 3.vi.1913 — in the Loveridge garden), 145 mm., breadth 109 mm., height 73 mm.

Carapace length of a ♀ (M.C.Z. 1498) from Algeria, 192 mm., breadth 133 mm., height 100 mm., far surpassed by an Algerian ♀ 276 mm. (see below) mentioned by Flower (1945:452) who points out that the largest examples of this species may not be more than 35 years old, though attaining a much greater age. Moreover, he says that very large individuals of this *species* need not necessarily have come from the Balkan Peninsula or Asia Minor, but may sometimes be of the typical North African race.

Growth and Weight. The carapaces of two tortoises of uncertain origin (purchased from a dealer in Norwich, England) increased during a seven-year period from 7 to 9, and 7½ to 9½ inches, respectively, when measured over the curve. Their weight, recorded every six months from 1886-1892, showed a gain of 11 and 12 oz., respectively. Occasional fluctuations in the carefully tabulated figures were attributed to variations in the

[1] Under 65 mm. according to Strauch (1862b:15); occasionally movable in young (Koenig:1892).

[2] Very slightly (Schlegel:1841); observable in the largest adults (Strauch: 1862b); sufficiently movable in ♀♀ to facilitate enlarging the opening (Doumergue:1899); movable in both sexes (Siebenrock:1906c).

climatic conditions, hot summers and cold winters being considered as the most favorable for growth by Sir Peter Eade (1893) whose papers contain a wealth of detail.

Flower (1945:451) furnishes the annual weights and measurements of two female Algerian *graeca* that were hatched in September, 1905, from a batch of 14 eggs laid the previous May. Of the 14 hatchlings, two were acquired by C. F. Moysey on 22.ii.06. The following day he weighed and measured them for the first time and gave them the names of "Daimler" and "Panhard." Their respective weights were then .008 (Daimler) and .012 kgm. (Panhard), their carapacial lengths *over the curve* 47 and 49 mm. respectively. During the succeeding 39 years (in Somersetshire and Devon gardens) a fairly regular rate of growth (measurements were not taken from 1921 to 1937) was maintained while, except on two occasions, each tortoise registered an increase in weight *every* year from 1906 to 1944. In the latter year their respective weights were 1.814 and 3.969 kgm., their corresponding lengths over the curve 279 (11 inches) and 365 mm. (14⅜ inches). In a straight line the length of the latter (Panhard) was 276 mm. (10⅞ inches) on 22.v.44. Of its weight Flower remarks that it was (almost) the same as that of the heaviest *graeca* in the Giza Zoological Gardens, which he recorded as 4 kilos (8 lbs. 13 oz.).

Following the exceptionally fine and dry summer of 1955, which probably stimulated the tortoises' appetites, Daimler and Panhard were weighed on September 1st *for the fiftieth successive year* of their captivity. At that time Daimler weighed 2.629 kgm., and measured 298 mm., having ceased growth in 1949 at 44 years, while Panhard weighed 4.252 kgm., and measured 365 mm., having ceased growth in 1942 at 37 years. The weight of the larger tortoise may well constitute a record for a North African *graeca*. Certainly Mr. Moysey's achievement in weighing these animals monthly, except when hibernating, for half a century is something for which all herpetologists should be grateful. For the supplementary data contained in this paragraph we personally are indebted to Mr. Moysey (in letter of 14.i.56).

Mr. Moysey suggests that the difference in size of his two female tortoises is possibly attributable to the sharper-edged beak of the larger. With a single snap this reptile would sever a piece

of leaf, whereas the smaller specimen often made several abortive attempts before succeeding in separating a piece for mastication and swallowing.

Sexual dimorphism. Eighteen alleged secondary sexual characters are discussed and illustrated by Camerano (1877:pl. lv). Most, if not all, are highly questionable. Werner (1895c) states that sex cannot be determined by plastron for he says it may be concave, flat, or slightly convex in either sex.

Courtship. Burton (1953:34) quotes C. H. Lay as saying that sometimes between mid-May and mid-June a thirty-year-old captive "*ibera*" male annually executes a series of rhythmic convolutions which leave a definite and regular pattern (cf. fig. in Burton) on the bare soil over an area of about forty feet square. The course taken is not so obvious in years when grass or weeds cover the plot. If this is indeed a courtship performance, supplementary to the oft-recorded butting described below, then further information should be gathered by persons resident in Africa.

Breeding. Possibly the fullest account of the breeding of a Moroccan tortoise is furnished by Gaston Astre (1948:60-64), based on a young and an adult ♂ and an old ♀ that had lived in his garden at Toulouse for twenty years. Owing, perhaps, to the difference in age and size of the ♂ ♂, no combats were observed between them. However, each spring the adult ♂ assiduously pursued the ♀. Then, rising on his four feet and withdrawing his head, with the front of his carapace he would deliver a smart blow on the back of hers. This performance would be repeated at the rate of one or two blows every two seconds. Should the ♀ hurry away the ♂ would give chase and, passing, bring her to a halt by biting at her head and forelimbs until she withdrew them within her shell, or, more usually, he would seize her carapace in his jaws and shake it with a range of as much as one or two centimetres. During copulation, according to Bailly-Maitre (1928), the male gapes widely and emits a muffled whistling cry.

From mid-May to mid-June the instincts of the ♀, rather than necessity, caused her to excavate with her hind feet a number of shallow troughs — about 34 mm. deep. These she soon abandoned, making no attempt to fill them in. Eventually, about the 10th to 15th of June, she would select a sunny spot with southern aspect, most frequently at the foot of a wall where the soil was

sandy or loose and the ground likely to remain dry. There, using her hind feet, she would dig a conical, somewhat bell-shaped, pit, though its sides might be almost vertical if the earth happened to be well packed, to a depth of 70 or 100 mm. and a surface diameter of 120 to 140 mm.

On the bottom of this funnel she usually deposited 2, though occasionally 3, white, ellipsoidal eggs measuring 25 x 30 mm. and weighing from 13 to 14 grams. Next she proceeded to cover them to a depth of about 30 mm. with loose earth taken from that heaped around the periphery of the excavation. The hole was never entirely filled, for after the tortoise had smoothed over the surface a slight concavity of from 5 to 10 mm. remained. Having finished her task the tortoise would unconcernedly walk away.

On one occasion Astre noted the time expended on nest-making and egg-laying. Digging commenced at 12 noon and was completed at 17.30 hours. Laying began at 17.30 and continued until 18 hours. Covering the eggs and filling in the hole with earth took until 18.30, after which the tortoise made for the far end of the garden, where she customarily spent the night beneath a heap of dry vegetational debris, and went to sleep.

Though eggs were laid each summer for a period of twenty years they never hatched owing to the Toulouse climate. Following the unusually hot summer of 1947, however, when the average temperature for July was 23.02° C., for August 23.81° C., with a maximum of 42° on August 1st, and averaging 19.7°C. during September, two eggs hatched. It may be assumed that the temperature of the soil when directly exposed to the sun was possibly 20° higher than the shade temperatures cited above.

If the eggs benefited by the exceptionally warm summer, the hatchlings were favored by the unusually mild winter that followed. The average temperatures were 7.76°, 7.25° and 12°C. respectively for the months of January, February and March, 1948. In April, when the young tortoises would be about 6 months old, they weighed 9 grams apiece and their carapaces measured 30 mm. in length by 25 mm. in breadth.

In October, Bailly-Maitre (1928) found a hatchling Algerian tortoise in his Narbonne garden and, on examining the nest, a freshly dead embryo in an egg. Astre mentions that in Septem-

ber, 1944, M. LeCompte discovered in his Gironde garden a small tortoise that appeared to have been hatched there.

During the Tunisian rainy season in early spring, these tortoises are rarely in evidence unless the sun is powerful. When this happens the reptiles begin to wander about in search of each other (Chaignon:1904). On March 12th, in Algeria, tortoises were observed fighting and mating among the bushes (Doumergue:1899).

In May, 3 ellipsoid eggs, each the size of a pigeon's, were present in a Tunisian tortoise eaten by Chaignon (1904). An old ♀, captured in the Macta (Mactra) region on 19.v.1890, laid an egg on June 25th; on July 4th two more eggs were found, and laying continued until 7 eggs had been deposited (over how long a period is not stated). These eggs measured 28 x 36 mm. (Doumergue:1899). In August an Algerian tortoise laid 2 eggs measuring 24 x 33 mm. (Werner:1894), while others laid by a 202 mm. Tunisian reptile measured 24.5 to 31 x 31.5 to 38.5 mm. (Gadeau de Kerville:1908). An egg in our possession (M.C.Z. 19003) measures 26 x 37 mm. The remarks by Kercado (1875) are intentionally omitted as being based on untrustworthy hearsay.

Longevity. The record is given by Flower (1925b and 1937a) as being 102 or 125 years, depending on whether Archbishop Laud's tortoise died in 1730 or 1753. This reptile, whose shell was examined and identified by Flower at Lambeth Palace where it is preserved, was at Fulham Palace in 1628 when Laud was Bishop of London. He took it with him to Lambeth Palace when he became Archbishop of Canterbury in 1633. Much supplementary information regarding this and other historical tortoises will be found in the references given above.

Possibly more reliable records are those of 96 and 54 years down to one of 22 years, 10 months and 23 days for a tortoise (M.C.Z. 18161) already adult when brought back from Bone, Algeria, on 10.vii.1890. The latter lived until 3.vii.1913 when one of us (A.L.) chloroformed him because he was so weak and moribund that flies were buzzing around him and depositing their eggs about his tail. Each winter during his life in a South Wales garden, he had dug himself under the surface in a strawed-over strawberry bed.

Diet. Food is taken with a snapping movement or torn away, being swallowed with little or no mastication. When not fed, Eade's two tortoises sought, not grass but clover, trefoil and fleshy-leaved plants such as *Echweria* or *Sedum.* They displayed a marked preference for yellow blossoms, consuming quantities of buttercups, dandelions, French beans and lettuce. Both would leave all other food for a green pea, a vegetable of which they were so fond that they would follow anyone who would feed them peas and clamber up his legs in their eagerness to reach them. One would take sliced apple, the other not. While a neighbor's tortoise fed on milk-soaked bread, Eade's two could not be tempted with milk and never drank water (Eade:1886). Captive tortoises at St. Petersburg were fed cabbages and potatoes (Eichwald:1851).

Though essentially vegetarian, according to Doumergue (1899) they will take insects, mollusks and worms during the Algerian dry season! Street vendors are apt to advertise these tortoises as useful in ridding a house of cockroaches or a garden of slugs. As a result many perish of starvation unless liberated in a garden where they can help themselves to lettuce and strawberries.

Parasites. Ticks (*Hyalomma aegyptiacum* Linnaeus) from a Rabat tortoise were identified as its synonym (*Hyalomma syriacum* C. L. Koch) by Dr. R. Schweizer (Hediger:1935).

Enemies. Tortoise eggs are richer in albumen than those of birds; the flesh also is edible and tortoise broth is recommended for the feeble (Doumergue:1899). The flesh is like that of a chicken and many were eaten by the French soldiers, though not by the Arabs and Moors (Rozet:1833), for the latter fear them, imagining that they are evil spirits (Poiret:1789).

Formerly it was, and possibly still is a common sight in early summer in the larger cities of Europe, especially maritime ones, to see barrow loads of these helpless reptiles being offered for sale by street vendors, or crawling aimlessly about in the windows of so-called pet shops.

Temperament. Of three purchased from a hawker on a Norwich street by Eade (1886:316-322) one died, the others appeared ill but recovered. They showed little evidence of *hearing,* but their *sight* was acute and their sense of *taste* well developed, enabling them to "discriminate instantly." As Lady Eade was

apt to indulge them with their favorite foods, upon her arrival they would leave Sir Peter — even though he might be feeding them at the time — and go to her to be fed. They ate only once a day, if at all, during cool weather.

On the finest summer days, however, they were early astir and by 6 or 7 A.M. might be found nibbling at trefoil. Normally they did not venture abroad until between 8 and 10 o'clock, and not then if it happened to be raining or overcast. Should a cloud obscure the sun when they were feeding, both would promptly withdraw their heads. In thundery weather, even though there might be hot and sunny intervals, the tortoises remained quiet and indifferent to food. When the solar rays were insufficiently hot the reptiles would tilt themselves against the south wall of a greenhouse in order to enjoy the maximum warmth. When too hot they would bury their heads beneath leaves while leaving the carapace exposed.

They objected to being placed in a sleeping place other than the one to which they customarily resorted. In cool weather, however, Sir Peter habitually placed them under a mat in the greenhouse; next morning they would be at the door waiting to be let out. When shut up in a greenhouse one tortoise was frequently found mounted on the other's back or on an inverted flowerpot. Apparently both were ♂ ♂ but they did not fight or display any interest in each other's society; when one got in the way its companion would attempt to clamber over it. Both evinced a love of climbing; when one tried to ascend some sticks that were resting against a wall, it slipped and was found sprawling on its back, three legs waving helplessly in the air while only one hind limb rested on the ground.

If carried from some spot they liked, they would make straight for it again as soon as released. When timed it was found that one took a minute to walk 10 feet, while the other could do 20 feet in this period; at this rate they would take between 4 and 5 hours to cover a mile. Their *memories* appear good, for immediately after emerging from a hibernation of 7 to 8 months' duration, they would set off for their old haunts as if only a day had intervened.

Aestivation and Hibernation. Both aestivation and hibernation are intermittent in North Africa. During the Algerian summer

these tortoises normally seek shelter from the sun by burying themselves, and consequently are rarely encountered (Doumergue:1899), but in July and August two were collected in the early morning by Hediger (1928).

They reappear in September only to vanish again at the approach of winter by concealing themselves in burrows or beneath a large stone. Even in the depth of winter, however, when the ground has been sufficiently heated by the sun, individual tortoises emerge for a time. In the hot coastal dunes and hills they come out again in February (Doumergue:1899).

Habitat. In Algeria these tortoises are extremely common throughout the region from Oran to the Petit Atlas (Rozet:1833), where they occur among the dwarf palms (*Chamaerops humilis*) beneath whose fronds they conceal themselves (Schlegel:1841). They are numerous among the bushes (*Zizyphus jujuba*) that are scattered throughout the waste lands (Eversmann:1854), where they are more plentiful among the dunes than on the edges of the plains (Le Cerf:1907). Scarce, though widely distributed throughout the mountainous regions and all the high plateaus, this species is apparently absent from the oases, its most southerly records being Beguira; El Aricha, and Geryville (Doumergue:1899). Absent south of El Kantara (Kantarah), which is also the most southerly limit for the lizard genera *Lacerta*, *Ophisops* (*Ophiops*) and *Psammodromus* (Werner:1894).

Common on the plains of Tunisia (Olivier:1896b).

Localities. Spanish Morocco: Tangier (Tanger). *French Morocco:* Azemmour (Azimor); Azrou; *Beni Snassene; Berguent; Casablanca; Dar el Beida, Casablanca; El Marit, Casablanca; Fes (Fez); Karia ba Mohammed; Maarif near Casablanca; *Mamora (Marmorea) Forest; Mogador; Moghran, a confluent of Sebou west of Beht; Oued Akrech, south of Rabat; Oued Mella north of Mogador; Ouezzane; Rabat (Aïn el Anda and La California); *Sefrou; Sidi Amar; *Sidi Yahia (U.S.N.M.); Souk el Arba; Taourirt. *Algeria:* Aumale, Guyotville; Bainen Forest near Algiers, Batna; Beguira; Biskra; *Bone; Boudsareah near Algiers; Bou Saada; Constantine; El Aricha; Geryville; La Calle; Lambeze (Lambesa); Macta; Maison Caree near Algiers; Medea (Medeah); Metidja near Algiers; Nemours; Palestro; on mountains

between Rosmarin and Thymian; Santa Cruz=Oran. *Tunisia:* Aïn Draham; Bir Mcherga; Djebel Achkel (? Ischkeul); Djebel Rsass (*sic*); Douirat (Duirat); Graiba; Kairouan (Kairwan); Maxula Rades; Sidi bou Ali; Tunis; Utique ruins; Zarzis. *Libya:* Barce (= El Merg); Bengasi; Bir (Bil) Milrha; Marmarica; Merg (= Barce); Tobruk (Tobruch); Tolmeta (Tolmetta); Tripoli.

Range. Morocco to Cyrenaica; Pityusen Islands and southern Spain.

Pseudotestudo new subgenus

Type species: *Testudo kleinmanni* Lortet

Definition. Supracaudal usually single. Maxillary without ridges; anterior palatine foramina large, not at all concealed; quadrate not enclosing stapes. Plastron of adults with a clearly movable posterior lobe in both sexes. Tail claw absent.

Range. Northeast Africa.

Testudo kleinmanni Lortet

1823. *Testudo graeca* Lichtenstein (not of Linnaeus), 91.
1835. Rüppell, 4.
1880d. Peters, 305.
1881a. Peters, 365.
1835. *Testudo marginata* Duméril and Bibron (part: not of Schoepff), 37.
1844. Gray, 9.
1855. Gray, 11.
1857. Jan, 35.
1855. *?Chersus mauritanicus* Fitzinger (not of Duméril and Bibron), 252 (Egypt).
1869a. *Testudo leithii* Günther, Proc. Zool. Soc. London, p. 502, figs. 1-4: "Sindh" (error); preoccupied by *T. leithii* Carter, 1852.
1869b. Günther, 110.
1880c. Vaillant, 32, 88.
1889a. Boulenger, 175.
1890. Boulenger, Fauna British India. Rept. and Batr., p. 20.
1890. Strauch, 45.
1892. Baur, 156.
1893a. Boettger, 11.
1896. Anderson, 77, 95.

1898. Anderson, 28, col. pl. ii.
1901. Steindachner, 326.
1904. Andersson, 9.
1908b. Kammerer, 757.
1908c. Kammerer, 772, figs. 9-10.
1909a. Siebenrock, 540.
1909a. Werner, 596, 628.
1912b. Werner, 452.
1913. Ghigi, 283.
1923a. Calabresi, 7.
1924a. Flower, 920.
1925b. Flower, 928.
1926. Flower, 133.
1927. Vinciguerra, 328.
1929. Flower, 29.
1929. Zavattari, 86.
1930a. Zavattari, 263.
1931. Gestro and Vinciguerra, 538.
1933. Flower, 745, fig. 1a.
1934a. Mertens and Müller *in* Rust, 9.
1937. Zavattari, 530.
1950. Williams, 551.
1870c. *Peltastes leithii* Gray, 657.
1870e. Gray, 11, fig. 6.
1873b. Gray, 11.
1883. *Testudo Kleinmanni* Lortet, Arch. Mus. Hist. Nat. Lyon, **3**, p. 188: Lower Egypt and environs of Alexandria, Egypt.
1887. Lortet, 11, pl. v.
1894. *Testudo campanulata* d'Aubusson (not of Strauch), for 1893, 230.

Synonymy. Mons. Kleinmann, after whom the species is named, was Director of the Crédit lyonnais en Egypte (Lortet: 1887:13). *Testudo leithii*, named for Dr. A. H. Leith by Günther (1869a), is preoccupied by *Testudo leithii* Carter 1852 proposed for a fossil turtle from Worli Hill, Bombay, India, which Williams (1953)[1] has shown to be that of a pelomedusid and assigned to a new genus — *Carteremys*.

Common names. Egyptian Tortoise (suggested); Leith's Tortoise (Flower); *solhalfa* or *zihlifa* (Innes *in* Anderson 1898).

Illustrations. Exceptionally fine colored figures of this species (dorsal, lateral and ventral views) are given by Lortet (1887:pl. v) and Anderson (1898:pl: ii).

[1] Williams, E. E., 1953, Breviora (Mus. Comp. Zool.), No 13, p. 5.

Description. Beak feebly or moderately hooked, tricuspid; edge of jaws not dentate; supranasals present, sometimes meeting mesially; prefrontal entire, divided longitudinally, or broken up; frontal large or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with a few, contiguous, extremely large, imbricate, rounded or pointed scutes forming 3, rarely 4, longitudinal and 4-7 transverse series from elbow to outer claw; claws 5, rarely 4;[1] hinder side of thigh without enlarged tubercles; heel with large, conical, spurlike tubercle; claws 4; tail with or without a terminal clawlike tubercle.

Carapace convex, slightly depressed in young only, sides descending abruptly, deeply or broadly notched in nuchal region, anterior and posterior margins not expanded, not, or but slightly, serrated; dorsal shields concentrically striated, not or but slightly swollen; nuchal moderate or large, triangular, rectangular or exceptionally elongate;[2] vertebrals 5, rarely 6 or 7,[3] the first as broad as, or much broader than, long, smaller than the second to fifth which are narrower than, as broad as, or broader than, the costals;[4] costals 4, rarely 3 or 5,[5] not forming an angle with the marginals; marginals 11 or 12, rarely 10;[6] supracaudal usually undivided, less frequently divided, spread out like, but projecting angularly beyond, the marginals.

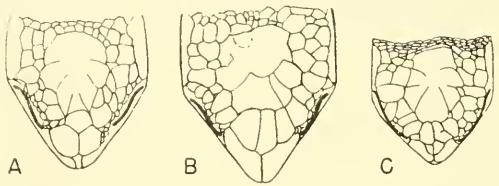


Fig. 22. Head scalation in *Testudo kleinmanni* (x 1). *A*, Salum specimen (M.C.Z. 54045); *B*, Salum specimen (M.C.Z. 54044); *C*, Alexandria specimen (M.C.Z. 5081), Cotype.

[1] Four in a tortoise bred at Giza Zoo from El Arish parents, both of whom had four claws only on each forefoot (Flower :1933 :747).

[2] In a ♂ from El Arish in which it was 6 mm. x 2.5 broad mm. (Flower :1933 : 747).

[3] Six in a hatchling and also in a 95 mm. ♂ from El Arish (Flower :1933 :747); seven in a cotype (U.S.N.M., 10979) seen by E.E.W.

[4] In a 95 mm. Derna tortoise the third vertebral has given rise to a couple of supplementary shields lying between the 3rd and 4th costals (Calabresi: 192 'a).

[5] Three in one seen by Flower (1953 :748); 5 on right side of a carapace (Y.P.M. 672) seen by us.

[6] Ten on one side of a cotype (U.S.N.M. 10979) and a specimen (B.M. 1922.5.23.2), both seen by E.E.W.; 12 in a 95 mm. ♂ from El Arish, while others from this locality had 11 on one side and 12 on the other (Flower :1933 :747).

Front lobe of plastron anteriorly truncate, not or but slightly produced, somewhat notched and each lateral point itself very slightly toothed; gulars paired, rarely absent;[1] pectorals moderate, their anterior border usually widening towards the axillary notch; axillary 1, moderate; inguinals 1 or 2, small or moderate, in contact with, or separated from, the femoral; hind lobe very broadly notched posteriorly, slightly movable in adults of both sexes but especially in the ♀.

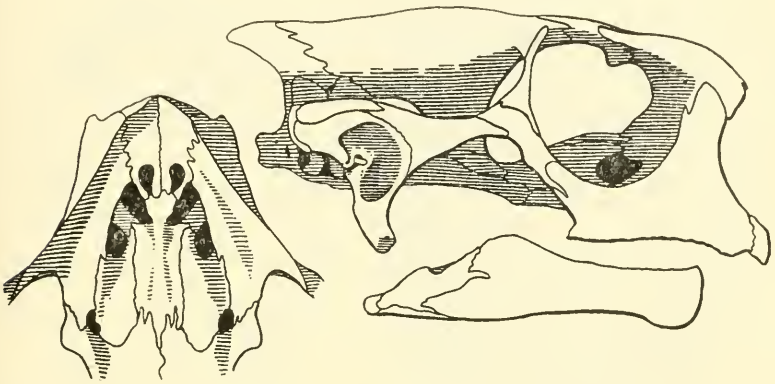


Fig. 23. Skull of *Testudo kleinmanni* (Yale Mus. 667). Condylobasal length 21 mm. The entrance of the parietal into the orbit is an individual peculiarity.

(S. McDowell del.)

Plastral formula: Abd > (g, h, p, an, subequal) > f.

Color. Carapace greenish yellow to pale yellow, uniform, or each shield more or less edged with black or brown. Plastron greenish to yellow, each abdominal shield with a dark brown to black, triangular or cuneiform patch, which is usually conspicuous and never entirely absent; pectorals occasionally margined anteriorly with dark brown; remaining plastral shields uniform. Hatchlings are completely yellow, according to Lortet (1887).

[1] Absent in a Giza tortoise (U.S.N.M. 55758) in which the anterior lobe is abnormally shortened though apparently *not* the result of an injury.

Head, neck, limbs, feet, nails and tail, yellow; rarely a black spot on crown of head posterior to the eyes; the buttonlike eyes strikingly black, the irides in both sexes being shining black and very conspicuous according to Flower (1933:748) who should be consulted for further details on coloration. His paper, based on 159 living tortoises, contains far more information about *"leithii"* than all of the other citations combined.

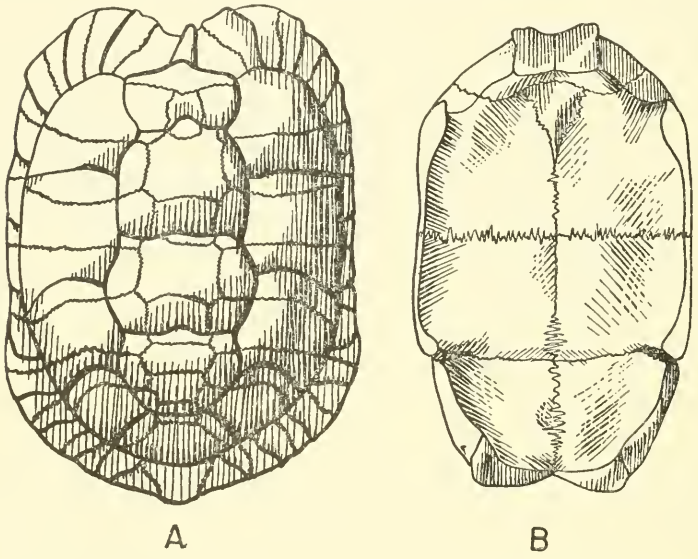


Fig. 24. *Testudo kleinmanni*. *A*, Dorsal view of carapace (M.C.Z. 1499) (x ⅔); *B*, Internal view of plastron (Yale Mus. 667). Note hinging of the posterior lobe (x ⅔).

(P. Washer del.)

Size. Carapace length of adult ♂ ♂ is from 86 to 110 mm.; the last mentioned, coming from El Arish, is exceptional for a ♂. Carapace length of adult ♀ ♀ is from 113 to 127 mm., the latter from Mersa Matruh (cf. Flower:1933:746). Carapace length of a ♀ (M.C.Z. 1499) 100 mm., breadth 72 mm., height 57 mm. Carapace length of a *kleinmanni* cotype, 100 mm., of the *leithii* holotype 120 mm.; of a juvenile *kleinmanni* cotype (M.C.Z. 5081) 55 mm., breadth 45 mm., height 28 mm.

Weight. Adults average 7 to 9 oz. (.198 to .255 kgm.), the largest attaining 13 or 14 oz. (.35 to .4 kgm.), *fide* Flower (1933:746).

Sexual dimorphism. Tail of ♀ short and pointed, that of the ♂ very long, yet exceeded by the fully extended penis which, though normally pink, then turns to a rich purple (Flower: 1933:746).

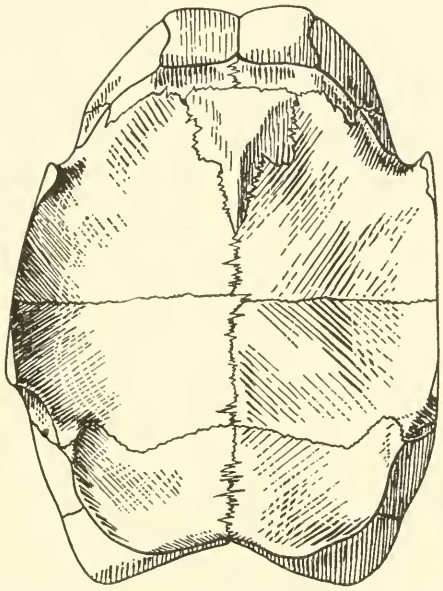


Fig. 25. *Testudo hermanni* ♂ (M.C.Z.). Internal view of plastron to show absence of hinging.

(P. Washer del.)

Breeding. Mating at the Giza Zoological Gardens, Cairo, took place in September and October (Flower). March and April among captive tortoises (Lortet:1883), while a ♂ that Kammerer (1908c) kept for five years, repeatedly copulated with captive *hermanni* (miscalled *graeca*) but, possibly because the ♀♀ were subadult, they remained infertile. Flower describes the voice of the mating ♂ as sounding like the intermittent winding-up of a metal spring.

Eggs with a rosy blush and measuring 23 x 30 mm., were deposited in May and abandoned on the surface, according to Lortet (1887), who adds that when the temperature is sufficiently high the young may emerge in 20 days after laying. Such hatchlings were completely yellow.

On two occasions eggs were laid at Giza in June, one laid on the 17th measured 22.75 x 29 mm. No records were kept as to when the majority of the eggs were laid, but 69 hatchings took place as follows: September (6); October (37); November (17); January (3); February (6).

Kammerer (1908b) somewhat vaguely refers to a dozen eggs measuring 22 x 28 mm., some of which were laid on July 6 by a tortoise having a carapace length of 104 mm. After 125 days[1] all allegedly hatched on November 8 but, refusing food, died within a few weeks of emergence. The dimensions of these hatchlings, stated to be from 18 to 19 mm., are at variance with those furnished by Flower (1933:748) for one which was 33 mm. in carapace length and 28 mm. in breadth.

The outline of *kleinmanni* hatchlings is quite different from that of the more spherical *graeca*. Contrasting figures to illustrate this are furnished by Flower (1933:748).

Longevity. Twenty-one years and 25 days. Average longevity of twenty tortoises still living in the Giza Zoo in 1925, was 16 years, 7 months, and 6 days (Flower:1925b).

Diet. Largely Saltwort (*Salsola* sp.) and Sea Lavender (*Limonium* sp.) according to Lortet (1887:14).

Hibernation. Active throughout the Egyptian winter though more sensitive to low temperatures than either *graeca* or *marginata*, according to Lortet (1887:14).

Habitat. In Egypt it is very restricted, being absent from the deserts around Cairo, and present only in two districts which are about 180 miles apart, viz. the northwestern deserts of the Nile delta and region of Suez Canal where, as well as in northern Sinai, it may be found among the bushes growing in the vicinity of brackish lagoons.

Localities. Libya: Barca; between Bir Sceferzen and Esc-Seegga on the Giarabub to Tobruk road; Sirtica; Wadi Tessina in Kufra Oasis. *Egypt:* *Alexandria; Bir el Abd; Damietta; El Arish (Arisc); *Giza (Gizeh); Ismailia; Kantara (Kantareh);

[1] Compare with Lortet above!

Khabra Abu Guzoar; Katia; Lahfan; Mariut (Maryut); Mersa Matruh; Port Said; Romani; Salmana; *Salum; Wadi el Amr; Wadi Hareidhin.

Range. Western Cyrenaica and northern Egypt (including northern Sinai).[1]

Genus MALACOCHERSUS Lindholm

1929. *Malacochersus* Lindholm, Zool. Anz., **81**, p. 285. Type: *Testudo tornieri* Siebenrock (by original designation).

Definition. Skull with triturating surface of maxilla strongly ridged; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina small, concealed in ventral view; prootic well exposed dorsally; quadrate enclosing stapes; surangular sometimes markedly lower than prearticular, exposing the latter to view externally; neck with third or fourth centrum biconvex.

Carapace never hinged, *persistently fenestrated; neurals attenuated and greatly reduced;* outer side of third costal scute about as long as, or longer than, that of fourth; submarginal scute absent; a single suprapygal.

Plastron never hinged, persistently fenestrated; gular region neither thickened nor produced; gulars paired, broader than long.

Distinguishing marks. No other tortoise is so nearly flat or has a shell so flexible that it may be compressed between finger and thumb. Carapace length not known to exceed 177 mm.

Range. Apparently restricted to certain rocky regions of Kenya and Tanganyika.

Fossil record. None.

Remarks. The relationships of *Malacochersus* are far from clear. At first glance the shell seems anomalous and unique, yet its fenestration, as has been made clear by Miss Procter (1922b), is similar to that of some adult *Gopherus polyphemus* and to the hatchling stages of every tortoise (cf. Procter: fig. 21b of a young *Testudo horsfieldi* and the figures in Gray: 1873e). In *Malacochersus* we find persisting into adult life a stage in shell

[1] Tristram's statement (1884, The Survey of Western Palestine, The Fauna and Flora of Palestine, 156) that *Kleinmanni* ranges northwards in suitable localities to the western side of the Black Sea (in the vicinity of Hebron), Palestine, was based on a misidentification as shown by Flower (1933:745).

ontogeny usually present only for a short time after hatching. At least this is true of the dermal shell. There is, however, some resorption of the endochondral ribs, but this also is paralleled in other land tortoises, in which reduction of the ribs is a very common condition. Apart from fenestration, the shell is rather primitive, i.e. essentially emydine, in its single suprapygal, the hardly developed gular lip and the broad transversely extended gular scutes.

However, skull, vertebrae and limbs are thoroughly testudinine and differ but little from those of *Geochelone*. Limbs and vertebrae are in fact in no way distinctive, but the skull has certain discernible but rather subtle peculiarities, and the mandible is more conspicuously distinct in a dorsal emargination of the surangular. This is not consistently present and while it is tempting to ascribe such an emargination to a general weakness of ossification in this form, such a suggestion is not borne out by the very solidly built skull in which even the anterior palatine foramina are not at all enlarged.

In external features *M. tornieri* is somewhat peculiar. The transversely, rather than longitudinally, developed gulars recall *Homopus*, while the head scutellation with its large supranasals along with the prefrontals and frontal, is more elaborate, so possibly more primitive, than that in any other form except *Testudo*. Miss Procter would call an azygous scute, occasionally occurring on the anterior plastron, an intergular, comparable to that of primitive turtles; it may be doubted that these anomalies have any atavistic or phylogenetic significance. The flatness of the shell is extraordinary and, as Dr. Procter comments, is unrelated to the fenestration but appears to be a special development correlated with the reptile's habits. Miss Procter believed the feet to be more supple at wrists and ankles and less club-shaped than in most testudinines.

Because of the nature of the shell the paleontology of this form is unlikely to become known soon. The best hope would appear to be a skull, since that is rather solidly built, but even this would have to be well preserved, and, as is well known, well-preserved turtle skulls are paleontological rarities.

In the preceding diagram of relationships (see p. 210) we have tentatively suggested *Malacochersus* as arising quite independ-

ently from the ancestral stock of the testudinines. It would seem that the characters possessed by *Malacochersus*, other than specializations peculiar to itself, are primitive for the subfamily. This opinion, while the best we can offer, is a guess, but on the basis of the data available no other conclusion seems likely.

Fig. 26. Distribution of *Malacochersus tornieri* in East Africa. The hollow circle indicates the type locality of *procterae*. (P. Washer del.)

The distribution of this peculiar genus, dependent on a rocky habitat, is not merely limited but discontinuous if judged by present records. The presence of such a shy and cryptozoic

creature may well have been overlooked, however, and some of the gaps in its range are certain to be closed when intervening areas are carefully searched.

The southernmost record, Lindi, whence came the second known specimen, is on the southeast coast of Tanganyika Territory almost 400 miles southeast of Dodoma, which appears to be the chief center of distribution. From Dodoma the species extends west to Tabora and north to Busisi (the original type locality of *tornieri*) at the southern end of Lake Victoria, and east to Lake Eyasi which is due north of Dodoma.

The most northerly record for which a specimen is available, Njoro, Kenya Colony, is approximately 200 miles due north of Lake Eyasi. Another record in Kenya is Malindi about 360 miles southeast of Njoro on the Kenya coast and as far from Dodoma as it is from Njoro. But *Malacochersus* is to be looked for still further north, for in 1914 the late R. B. Woosnam, when asked by Loveridge whether undescribed reptiles were still to be found in Kenya, replied that he had once come across two strange soft-shelled land-tortoises when on safari in the Northern Frontier District. Being on the march at the time, and having nowhere else to put them, he had popped them into a cooking pot being carried by one of the bearers. Later, on enquiring for them, he found they had been turned loose by his indignant cook. Woosnam added that he had never seen any similar tortoises during the many years he had spent in Africa.

Malacochersus tornieri (Siebenrock)

1896. *Cinicys* (*sic*) *belliana* Tornier (part: not of Gray), 2.
1903. *Testudo tornieri* Siebenrock, Anz. Akad. Wiss. Wien, 40. p. 185: Busisi, s. end of Lake Victoria, Tanganyika Territory.
1903b. Siebenrock, 442, pl.
1904a. Siebenrock, 29, fig.
1909a. Siebenrock, 538.
1911. Lönnberg, 7.
1913c. Nieden, 54.
1922d. Loveridge, 522.
1923g. Loveridge, 931.
1924b. Loveridge, 2.
1924. Wettstein, 201, figs. 1-2.
1928d. Loveridge, 49.
1929. Flower, 32.

1933h. Loveridge, 207.
1936. Kanberg, 187, photo.
1936h. Loveridge, 19.
1936j. Loveridge, 221.
1937f. Loveridge, 492, 495.
1937. Ruckes, 103.
1940. Conant and Downes, 48.
1950. Williams, 550, 551.
1954. Noël-Hume, 76 (numerous misstatements).
1920e. *Testudo Loveridgii* Boulenger, C. R. Acad. Sci. (Paris), 170, p. 263: Dodoma, Ugogo, Tanganyika Territory.
1920d. Boulenger, 68.
1920. Boulenger, E. G., 190.
1921d. Loveridge, 50.
1922b. Procter, 483, figs. 1b, 2-11a, 12-21a, pls. i-iii.
1922d. Loveridge, 522.
1923g. Loveridge, 928.
1924b. Loveridge, 2.
1924b. Mertens, 71.
1924. Wettstein, 201, figs. 1-2.
1924d. Witte, 48, 61.
1925b. Flower, 925.
1922b. *Cinixys belliana* Procter (not of Gray), 515.
1923g. *Testudo procterae* Loveridge, Proc. Zool. Soc. London, p. 928, pls. i-ii: Ikikuyu, s. of Gulwe, Tanganyika Territory.
1924b. Loveridge, 2.
1924b. Mertens, 72.
1924d. Witte, 48, 62.
1937f. Loveridge, 495.
1929. *Testudo* (*Malacochersus*) *tornieri* Lindholm, 285.
1934a. *Malacochersus tornieri* Mertens and Müller *in* Rust, 9.
1937d. Mertens, 3.
1939. Zangerl, 355, 399, pl. ii.
1942d. Mertens, 245-251, figs. 1-4.
1949. Conant and Hudson, 4.
1949b. Loveridge, 19.
1934a. *Malacochersus procterae* Mertens and Müller *in* Rust, 9.

Further citations of "*tornieri*" will be found under *Kinixys b. belliana*.

Common names. Soft-shelled Tortoise (Flower); Pancake Tortoise (W. M. Mann).

Illustrations. Siebenrock (1903:pl. –) furnishes a dorsal view of the type of *tornieri*, together with detailed drawings of the

beak and scaling on the forelimb. Procter (1922:pl. i) has a colored plate of topotypical *loveridgii,* which should be contrasted with that of *procterae* as shown by Loveridge (1923g: pl. i). Siebenrock (1904a:fig. –) pictures the skeletal carapace from below; x-rays of ♂ and ♀, besides numerous developmental figures, will be found in Procter (1922b), Loveridge (1923g:pl. ii), and Zangerl (1939:pl. ii).

Types. The Berlin type, collected by Stuhlmann, was at first referred to *Kinixys* by Tornier under the impression that the paperlike consistency of its carapace was abnormal, perhaps a case of arrested development. Later Siebenrock (1903a), discov-

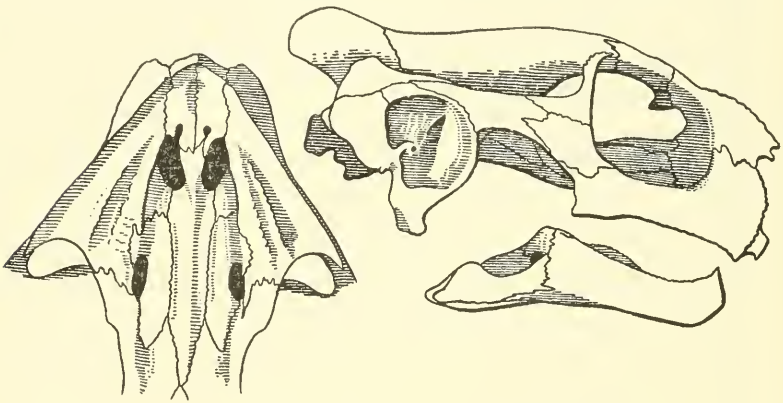


Fig. 27. Skull of *Malacochersus tornieri* (A.M.N.H. 45081). Condylobasal length 30 mm. The lateral exposure of the prearticular is not constant. (S. McDowell del.)

ering this Berlin specimen was not a *Kinixys* but an undescribed species of *Testudo,* named it *tornieri,* though still attributing its peculiar softness and flatness to pathological defects which had retarded the development of the bony carapace and plastron; alternatively he postulated faulty preservation. The receipt of a second specimen from Lindi, enabled him (1904a:29) to amplify his original description and give a detailed account of the fenestration of the shell.

When five specimens collected by one of us (A.L.) and labeled "*Testudo tornieri*" in the field, were submitted to Boulenger, he

regarded them as separable and distinct. Included in the shipment were other tortoises including a young *Kinixys belliana* from another locality which Boulenger (1920c) unfortunately assumed was the young of his *loveridgii*.

The disposition of *Testudo procterae* Loveridge, poses something of a problem. Its type locality — Ikikuyu (not to be confused with the place of the same name on the outskirts of Dodoma) south of Gulwe (Igulwe) Station on the Central Railway — is about 75 miles southeast of Dodoma, type locality of *loveridgii* Boulenger (=*tornieri*).

The supposed structural differences offer but weak support (cf. comments under Size) to the idea that the very distinctively colored (cf. Loveridge:1923g:col. pl. i.), but still unique, type of *procterae* in the British Museum is a distinct species. In the absence of more material, therefore, we incline to the view that *procterae* may be only a very striking color variant of *tornieri*. This view, if correct, is paralleled by the somewhat similar case of *"Homopus" bergeri* Lindholm, which we regard as merely a color variety of *Psammobates tentorius verroxii* (Smith). In both instances pattern reduction has taken place; in *bergeri* there has been a melanistic simplification; in *procterae* brown pigmentation has become dominant to the exclusion of all other markings.

However, in its *elongate* and large prefrontals with correlatively absent supranasals (cf. Plate 6), the head scalation of *procterae* differs strikingly from, and is not approached by, any of the many *tornieri* we have examined (cf. characteristic scutellation of *tornieri* in Fig. 19). Symmetrical as is the arrangement in the holotype of *procterae* there remains the possibility that it is an individual variation. Variation in head scalation, common though it is among tortoises, usually consists in a breakdown of the normal arrangement, *not in the appearance of an alternative pattern*. In this instance, with only a single specimen available, it is impossible to evaluate the importance of this character. It emphasizes the importance of securing further *Malacochersus* from the type locality of *procterae;* we have attempted to have such material obtained for us, but the attempt was unsuccessful.

Description. Beak weakly or moderately hooked, bi- or tricuspid, edge of jaws minutely denticulate; a pair of supranasals

in contact, very rarely separated; prefrontal entire or divided longitudinally or somewhat broken up; frontal large, small, or broken up; remaining upper head shields small, irregular; forelimb along anterior edge with some moderately enlarged, more or less imbricating scutes[1] forming about 5-10[2] transverse series from elbow to outer claw; on inner aspect of forelimb are 2-4 prominent, enlarged, separated or juxtaposed, pointed scutes; claws 5, occasionally 4 through accident; hinder side of thigh with a rosette of enlarged scales surrounding a somewhat larger subconical tubercle; heel sometimes with trace of a spurlike tubercle; claws 4; tail without terminal clawlike tubercle.

Carapace very much flattened dorsally, flexible, its sides either straight and parallel or oblique, perpendicular or steeply sloping, scarcely notched in nuchal region, anterior margin flat and weakly serrate, lateral margins sometimes reverted, gutterlike, posterior margin flat, rarely reverted, slightly serrated; dorsal shields concentrically striated, sometimes swollen;[3] nuchal somewhat broader than long in young, usually elongate in adults, anteriorly indentate and projecting, usually broader posteriorly, occasionally completely divided;[4] vertebrals 5 rarely 4,[5] 6,[6] or 7,[7] sometimes flat, very rarely divided longitudinally[8] or transversely,[9] the contact between fourth and fifth frequently very narrow, first vertebral slightly broader than long or as broad as long and smaller than the second to fifth, which are much broader than long, as broad as, or broader than, the costals; costals 4, rarely 5,[10] sometimes forming an angle with the lateral marginals; marginals 11, sometimes 12; supracaudal divided, sometimes above only, rarely undivided, downwardly directed or outwardly flared irrespective of sex.

[1] These enlarged scutes are both more numerous and strongly imbricating in the Njoro tortoise (Stockholm Mus.).

[2] Twelve on both sides of the Njoro specimen (Stockholm Mus.).

[3] Swollen in only one Dodoma individual (M.C.Z. 24912).

[4] Divided in a ♀ (M.C.Z. 30009) from Mangasini, and in U.S.N.M. 72505, probably from Dodoma.

[5] Four in a ♂ cotype of *loveridgii* (cf. Procter :1922b :fig. 4).

[6] Six in a ♀ (M.C.Z. 23000) from Kondoa Irangi.

[7] Seven in U.S.N.M. 73934, probably from Dodoma.

[8] Fourth vertebral is longitudinally divided in U.S.N.M. 72497, probably from Dodoma.

[9] Fifth vertebral is transversely divided in U.S.N.M. 73943, probably from Dodoma.

[10] Five in U.S.N.M. 72522, 73934, etc.

Front lobe of plastron anteriorly truncate, more or less produced, openly notched; gulars paired, as wide as, or wider than, long; exceptionally an intergular;[1] pectorals moderately broad, not or but slightly narrowed medially, their anterior border usually straight, widening gradually towards the axillary notch; axillaries 2, rarely 3, small; inguinals 2 to 4, outermost normally triangular, the others transverse, the innermost in contact with the femoral; hind lobe more or less deeply notched posteriorly.

Plastral formula: Abd>h>p>or<f>or=g>or=an.[2]

Color of a hatchling (M.C.Z. 18167). Ground color of carapace pale yellow; sutures between dorsals irregularly, but broadly, bordered with dull brown though frequently interrupted at one or more points on each shield; vertebrals 2 to 4 have a median brown spot, while the first and fifth vertebrals and each of the costals have a fainter, less regular, brown spot; dorsal edge of marginals with a less well-defined brown border tending to extend downwards between each marginal, free edge of marginals without markings. Plastron pale yellow, immaculate.

Color of juveniles. No two specimens are quite alike. Ground color of carapace pale yellow; brown borders covering the sutures become black, and both these and the inner brown borders tend to be interrupted to a varying extent by yellow rays, the brown spots on the vertebrals and costals may, or may not, persist. Plastron pale yellow, all the sutures, except those between the gulars and anals, dark brown crossed by light rays, while the gulars and anals may show a trace of such pigmentation. Plastron substantially as described below for adults.

Color of adults. Ground color of carapace pale yellow to horn with variable markings so that scarcely two are alike; dorsal pattern almost always more or less distinctly rayed like members of the *Psammobates geometricus* group with the rays tending to be much less regular, center of areola yellow surrounded by very irregular traces of brown while immediately outside the areolar area is a narrow zone of yellow, beyond which to the periphery of the shield is a broad black border broken by fine or broad yellow rays, sometimes one color, sometimes the other predominating according as the light rays are broad or narrow,

[1] Figured by Procter (1922b:495:fig. 7), also present in U.S.N.M. 72530 and 72547, probably from Dodoma.

[2] Gular smaller than the anal in the Njoro tortoise (Stockholm Mus.).

heavy or faint. Plastral shields with yellow areolae which may be smudged with brown; around the areola a broad zone of black, broken to a greater or lesser extent by yellow rays, in some cases, extends to the periphery of the shield, while in others it is separated from the periphery by a narrower or wider zone of yellow. In certain extreme cases the plastral shields appear almost black, in others mostly yellow. Very rarely a specimen may be almost uniform horn color both above and below.[1]

Size. Carapace length of a large ♂ (M.C.Z. 30008) 145 mm., breadth 102 mm., height 32 mm.; the corresponding figures for a ♂ cotype of *loveridgii* (Brit. Mus.) being 140 mm., 100 mm., and 27 mm. Carapace length of largest ♀ (M.C.Z. 23024), 177 mm., breadth 131 mm., height 40 mm.; the corresponding figures for the ♀ type of *tornieri* (Berlin Mus.) being 160 mm., 110 mm., and 35 mm., while those of the juvenile type of *procterae* (Brit. Mus.) are 85 mm., 72 mm., and 40 mm.

When *procterae* was compared with a *tornieri* of exactly the same carapace length, a difference in its relation to the breadth (84.5%) and depth (47%) was noted, the same figures for the *tornieri* being 90.5% and 26% respectively. However, at least in the breadth/length ratio *procterae* is within the range of Dodoma *tornieri* which ranged from 71 to 83.8% in seventeen specimens measured by Procter, and from 69.1 to 94.2% in twenty-five others measured by Loveridge.

Breeding. Courtship consisted in the ♂ impatiently snapping at the limbs of the ♀ as he followed her about, at times clambering on her back and biting viciously at her head whenever she ventured to thrust it out. Two ♂ ♂ were so ill-tempered as to seize the edges of the ♀ ♀ carapaces in their jaws, drag them along and eventually get beneath as they apparently attempted to overturn them. One ♂ persistently, though unsuccessfully, endeavored to mate with a ♀ *Kinixys b. belliana* which shared the enclosure. Pairing took place in January and February, as early as 9 A.M. and as late as 4.30 P.M.

Females appeared gravid in April. A single elongate egg is laid in July or August in East Africa, but Conant and Downs (1940:48) record an egg weighing 33.5 gm., and measuring 28 x 48 mm. being laid in the Philadelphia Zoo on January 9, 1937.

[1] As in U.S.N.M. 73945.

Two eggs removed from the enclosure at Kilosa, where they had been buried beneath a rockery, measured 26 x 42 mm. and 28 x 44 mm. The shells were extremely thin and brittle but one (M.C.Z. 43834) was successfully drilled and blown. On December 19, 1922, an embryo on the point of hatching was removed from another egg and preserved (M.C.Z. 18167).

Longevity. The Soft-shelled Tortoise is very hardy in captivity. One captured December 8, 1918, and taken to England in midwinter, lived in the Zoological Gardens, London, until July 2, 1927, i.e. 8 years, 6 months and 24 days in captivity (Flower, 1937, records only its stay at the zoo). Conant and Hudson (1949) mention one that lived at Philadelphia Zoo for 7 years, 5 months and 6 days.

Diet. Apparently Soft-shelled Tortoises emerge to feed only during the early morning hours. At Tabora one was found nibbling dry grass. In captivity they throve on lettuce and tender cabbage leaves or, for long periods, were fed on bread soaked in jam (Loveridge). Bread soaked in milk was taken, also clover, dandelion and lettuce; fruit only sparingly and they refused bananas altogether. The species is exclusively vegetarian (Mertens: 1942d).

Parasites. A tick (*Amblyomma nuttalii*[1]) was on the type of *procterae* when found. None of the extensive Dodoma series was so affected but soon acquired ticks when transported to Kilosa.

Habits. At 9 A.M. some young were found basking on a rock slab, though usually during daylight these tortoises spend their time in rock crevices into which they climb. Their depressed shells enable them to push their way farther into such retreats than if they were convex. When surprised suddenly the reptiles may be removed with ease, but if warned by a shadow falling across the entrance, they inflate their lungs so that their shells press upon the rock both above and below as they brace their legs like struts. Under these conditions it frequently took as much as an hour to work a single tortoise loose (Loveridge).

Eleven were found beneath one flattish slab of rock in January, possibly aestivating as that and February are the hottest months at Dodoma. In conformity with their structure, these tortoises are far more active than their allies of the genus *Geo-*

[1] Originally identified as *marmoreum* by S. Hirst; identification corrected by J. C. Bequaert.

chelone, while their predilection for clambering up and falling off rocks calls for rapid recovery in turning over should they land on their backs. In captivity they displayed surprising agility in climbing up vertical wire netting two feet in height, and many escaped. At night shelter was sought beneath the rockery where they would pile up on top of one another (Loveridge).

Mertens (1942d) found his captive specimens, though not nocturnal, spent most of the daylight hours in their hiding place. Even when feeding they did not venture more than nine metres from their retreat, which is definitely selected and constantly used thereafter. To it the tortoise hastens when surprised in the open, for *M. tornieri,* unlike most tortoises, does not, or only momentarily, withdraw its head inside its shell, preferring to make a dash for its home. This it locates in a matter of minutes if taken to a distant corner of the enclosure and then released. Also, after being removed to winter quarters, when liberated in the spring it readily located its "home."

Habitat. Small hills with rocky outcrops in arid thornbush or savanna, at altitudes from about 100 to 4000 feet. The most unusual habitat record was that of a tortoise taken by an African when "cleaning round his rice plants about a hundred yards from" Allen Turner's camp at Mida Creek.

Localities. Kenya Colony: 10 miles south of Malindi at Mida Creek; Mathews Range (*fide* J. G. Williams); Njoro. Tanganyika Territory: Busisi (Bussisia); Dodoma; Ikikuyu; Kibakwe; Kidengi; Kikombo; Kondoa Irangi; Lindi; near Lake Eyasi (as Njarassa); Mangasini; Matete; Mfilima; Tabora; Usandawi.

Range. Kenya Colony (in suitable terrain from Njoro east to Malindi) south to Tanganyika Territory (from Busisi, Smith Sound, Lake Victoria southeast through Ugogo to Lindi on the southeast coast).

Genus PSAMMOBATES Fitzinger

1835. *Psammobates* Fitzinger, Ann. Wiener Mus., **1**, pp. 108, 113, 122. Type: *Testudo geometrica* Linnaeus (designation by Fitzinger, 1843, Syst. Rept., part 1, p. 29).

1933b. *Chersinella* Hewitt (not of Gray: 1870), Ann. Natal Mus., **7**, p. 259. Type: *Testudo geometrica* Linnaeus (by original designation).

Definition. Skull with triturating surfaces of maxilla and premaxilla without ridging; maxillary participating in roof of palate; anterior palatine foramina small, concealed in ventral view; prootic narrowly exposed dorsally; quadrate enclosing stapes; surangular subequal in height to prearticular; neck with third or fourth centrum biconvex.

Carapace never hinged; normally the anterior neurals hexagonal; outer side of third costal scute about as long as, or longer than, that of the fourth; submarginal scute absent; suprapygals 1 or 2, if 2 they are separated by a straight transverse suture.

Plastron not hinged; gular region scarcely thickened and produced; gulars paired, longer than broad.

Range. Bechuanaland Protectorate; Union of South Africa (Orange Free State and Cape Province); Southwest Africa.

Fossil record. None.

Remarks. When Lindholm (1929:284, footnote) stated that the genus *Testudo* (*sensu* Strauch, Boulenger and Siebenrock) was unique, not only among reptiles and vertebrates but in the entire Animal Kingdom, he was referring to the fact that it contained some species (citing *Geochelone gigantea*) that in volume and weight were several hundred times greater than such alleged congeneric species as "*fiski*" (i.e. *Psammobates tentorius verroxii*). This is one of the tortoises of the *geometricus* group, none of whose members is known to exceed 150 mm. in carapace length.[1] Re-examining the case, we have found that in addition to size the other characters of the *geometricus* group require its separation as a genus distinct from both *Testudo* and *Geochelone*.

The *geometricus* group is emydine-like in maintaining as a normal condition the hexagonal neural pattern that *Geochelone*, *Testudo* and *Gopherus* — all three independently — abandoned (except as an occasional variant) 30 or more million years ago. In the general discussion of testudinine genera above (p. 218) the *geometricus* group (as *Psammobates*) was assigned to the larger assemblage of which *Homopus* is a central member. The character of hexagonal neural pattern has been one reason for this assignment, but several other considerations have entered

[1] We have not seen any larger than this, but larger specimens of *geometricus* itself have been reported (p. 323).

into this decision. A discussion of the problems involved seems pertinent here.

Among African tortoises several groups of species occur which are evidently endemic, as species groups, to this continent. Neglecting *Malacochersus* which seems quite isolated, the rest have several features in common. None of them has any close relative or representative outside Africa or even in North Africa. All have the neural bones hexagonal or vaguely quadrate or irregular, never with the regular octagonal and quadrilateral pattern that is characteristic of all Recent tortoises outside the Ethiopian region. *Chersina* approaches the advanced pattern more closely than any other of this group but still only occasionally and imperfectly. In all, the maxillary triturating surfaces are without definite ridging. *Chersina* again is atypical but it has only a very feeble ridge which is more easily felt than seen. All except *Homopus* have the primitive single or transversely divided suprapygal, not the geochelonide type. In addition all are of only small to moderate size.

Against these general resemblances are to be set the striking peculiarities which separate the African endemic species groups not only from each other but from everything else. We evaluate these peculiarities, as we have stated elsewhere (p. 218), as implying generic distinction. Yet it may be worth consideration that despite these peculiarities there have been instances of taxonomic confusion. For example, a color variant of a member of the *geometricus* group was described as a species of *Homopus* (*H. bergeri* Lindholm), and juvenile specimens of *Kinixys* with the carapacial hinge still undeveloped have been twice confused with *Homopus* (*H. nogueyi* Lataste and *H. darlingi* Boulenger). Though inability to separate forms is not always indicative of relationship, such errors at least make clear that the characters used to separate generic groups are not conspicuous always or at all ages. On our part, we believe that the resemblances of the African endemics to one another are really indicative of close relationships among them. We regard these endemics as a true autochthonous African group.

At this point it is necessary to mention the two endemic Malagasy tortoises — *Acinixys* and *Pyxis*. The skull of *Acinixys* has maxillary triturating ridges and its carapace has hexagonal

neurals. In *Pyxis* this situation is reversed, its skull lacking triturating ridges while its carapace shows the octagonal and quadrilateral neural pattern; in addition there is in *Pyxis* the obvious specialization of a very peculiar plastral hinge. Both possess the primitive pygal pattern, and in size they fit in the middle of the continental African series. Thus while seeming to resemble the continental African endemics, each of the Malagasy endemics differs from that series in a single character — in each case a different one. Note, however, that *Chersina* of continental Africa approaches each of these in precisely its aberrant character — *Acinixys* in its maxillary ridge and *Pyxis* in its approximations of an octagonal and quadrilateral neural pattern.

We interpret this case, as we have others, in terms of a conception of the evolution of tortoises as resulting from modifications in parallel occurring at very different tempos in the separate lineages and sub-lineages. Thus for the most part the Ethiopian endemics (including now the Malagasy with the continental African forms) have been slow to modify the primitive (emydine) neural and pygal patterns at the same time that most of them have gone the whole distance in the loss of maxillary ridging. *Acinixys* has been slow to evolve both maxillary and neural advanced features, while *Pyxis* has been "progressive" in both these details, but both *Acinixys* and *Pyxis* remain primitive in the pygal pattern in which *Homopus* has gone on to an advanced condition.

We see the Malagasy endemics therefore as part of one series with the African endemics — part thus of a larger autochthonous Ethiopian group. Recognition of such a group has a certain geographical tidiness, but there is very much more to support this conception than just this tidiness. We may argue from any one of the resemblances shared by these Ethiopian forms. Thus the primitive pygal pattern in an Ethiopian tortoise can be explained in one of three ways: (1) as an emydine inheritance going back to a separate emydine ancestor; (2) as an emydine inheritance shared with other Ethiopian tortoises and going back to a common ancestor; (3) a secondary reversion to a primitive condition. The likelihood of the first and third of these possibilities is much diminished by the occurrence of several forms with the same condition in one region, still further reduced by other resem-

blances among the forms. Thus, by elimination, the second of these suggestions appears to be the most likely. On the basis of primitive neural pattern an argument essentially identical may be set up, and a very similar argument will apply for the unridged maxilla. All of these taken together and considered along with the subtler cross resemblances among the forms would seem to strongly support the naturalness of our postulated group.

If this reasoning is valid and the Ethiopian endemics as a group do have a common ancestor independently of the other tortoises, then the *geometricus* group as one of this series cannot be retained in *Testudo*, at least not in any conception of tortoise genera short of an inclusive genus that would embrace the entire subfamily. *Below that level no inclusive genus would be at once definable and natural.* We do not argue against the genus-subfamily concept on grounds of merit, but to apply this viewpoint in only one subfamily would be to create a genus whose dimensions and variability are not consonant with those of the genera of any other subfamily or family in the order.

The argument that *Psammobates* must be separated from *Testudo*, as typified by *T. graeca*, does not automatically imply its distinctness from every other genus. We maintain it as separate because of its morphological distance from its closest relatives. Thus in skull structure *Psammobates* shows one feature in which it is distinctive within its lineage, and one that is altogether unique.

(1) The space between the ventral processes of the prefrontals is more restricted and, consequently, more emydine-like than in any other testudinine (Fig. 11 *H*, *I*). Indeed the opening in *Psammobates* approaches, but is still not quite as narrow as the widest narial apertures in emydines, e.g. *Hieremys* and *Siebenrockiella*. Since at least a moderate restriction of the narial aperture is probably primitive for all the Testudinidae (the emydine condition occurs in *Platysternon*), in this feature *Psammobates* is probably more primitive than any other living group of testudinines.

(2) Behind the anterior palatine foramina of *Psammobates* the maxillary bones send up into the roof of the palate more or less sizable wings which, from each side, approach, but never join, the vomer. This is decidedly a specialization.

In its shell structure, *Psammobates* displays a condition (in certain subspecies in very exaggerated form) unique among the African endemic genera — conically raised vertebrals. This condition, together with a very similar color pattern, occurs in some *Geochelone*, notably in *G. elegans* of Asia, but conical vertebrals also occur in *G. pardalis babcocki* and some South American tortoises. We consider this similarity convergent only, not more significant than the superficial similarity of *Emydoidea* with *Emys*, or the convergent resemblance of various agamid and iguanid lizards.

Differences in skull and shell as great as these seems to merit generic separation. Such recognition has already been accorded the group by Hewitt and other students of South African tortoises. The name *Chersinella* Gray, 1870, was at first employed by Hewitt. Unhappily this is doubly invalid, first because its genotype, as selected by Lindholm in 1929, is *Testudo gracca* Linnaeus, and also because a much older name is available. The correct name *Psammobates* Fitzinger, 1835, with *T. geometrica* Linnaeus as genotype, was subsequently adopted by Hewitt (1937e). The gender of *Psammobates* being masculine, it compels changes in termination of all the familiar names of the *geometricus* group.

General Survey of the *Psammobates* Species

No group of tortoises has fostered the making of so many specific names as has *Psammobates*. For the three species that we recognize there are 32 names available (see following list). This plethora of names provides examples of nearly every kind of taxonomic error. Names have been applied to adults and young separately (*geometrica* and *luteola; semiserrata* and *oculifera*). Names have also been erected: (1) due to the misreading of a type description (*smithi* Boulenger); (2) for striking color variants (*bergeri* Lindholm); (3) for striking scute variants (*strauchi* Lidth de Jeude); (4) for minor scute variants (*boettgeri* Siebenrock); (5) for ill-defined local populations (various names of Hewitt); (6) for selected series within a single local population (other names by Hewitt); (7) for intergrading populations (names by Hewitt).

Most of these unnecessary names apply to a single species — *tentorius* — individuals of which show an astonishing range of pigmentary and morphological variation. The errors of such earlier workers as Boulenger and Siebenrock resulted primarily from a lack of adequate series with definite locality data, their "new species" being based on one or very few specimens.

The extraordinary multiplication of names by Hewitt had a very different foundation — a philosophy of naming which we regard as unfortunate. Finding, when dealing with fairly large local collections, that he was more or less able to recognize members of these local series, Hewitt provided each such population with a formal Latin name. When these populations proved less homogeneous than usual, Hewitt proposed additional names for the extreme types, e.g. the three names given variants within the Hanover District population.

A list of names proposed for members of the genus *Psammobates* (Table 5) is offered as a ready means of recognizing the status assigned to each in this revision.

Grouping of Species

As suggested by Siebenrock (1904 and 1910), the species of *Psammobates* fall into two groups distinguished by the size of the nuchal, the number of the axillaries, and the plastral pattern. As is usual in testudinines every one of these characters is subject to individual variation, so that occasional individuals appear to transgress their group boundaries in one or another of these characters.

The first species group within *Psammobates* consists of two allopatric forms — *geometricus* and *oculifer*. Both differ from the *tentorius* complex in having a plastral pattern that covers the entire plastral area. Typically it is an elaborate rayed pattern in both *geometricus* and *oculifer,* but in the first it may sometimes be simplified (see Hewitt :1933b, pl. 14, fig. 6), and in the second it is sometimes indistinct. Both forms have only one axillary, but in *oculifer* it is almost always fused with the humeral (Fig. 30*B*).

Normally the nuchal shield is well developed and longer than broad in both species, more consistently in *oculifer* where it is regularly large and subtriangular. In *geometricus,* while usually

Table 5

Chronological List of Specific and Subspecific Names Proposed for Members of the "*geometricus* Group," (i.e. *Psammobates*), and their suggested Synonymy.

C. = *Chersinella*; *H.* = *Homopus*; *P.* = *Psammobates*; *T.* = *Testudo*

1.	*T. geometrica* Linnaeus, 1758	= *P. geometricus*
2.	*T. luteola* Daudin, 1802	= *P. geometricus*
3.	*T. oculifera* Kuhl, 1820	= *P. oculifer*
4.	*T. tentoria* Bell, 1828	= *P. t. tentorius*
5.	*T. verroxii* Smith, 1839	= *P. t. verroxii*
6.	*T. semiserrata* Smith, 1839	= *P. oculifer*
7.	*T. geometrica* var. *tentoria* (*non* Bell) Gray[1]	= *P. geometricus*
8.	*T. geometrica* var. *nigriventris* Gray, 1855	= *P. t. tentorius*
9.	*T. trimeni* Boulenger, 1886	= *P. t. trimeni*
10.	*T. smithi* Boulenger, 1886	= *P. t. verroxii*
11.	*T. fiski* Boulenger, 1886	= *P. t. verroxii*
12.	*T. strauchi* Lidth de Jeude, 1893	= *P. geometricus*
13.	*T. seimundi* Boulenger, 1903	= *P. t. verroxii*
14.	*T. boettgeri* Siebenrock, 1904	= *P. t. verroxii*
15.	*H. bergeri* Lindholm, 1906	= *P. t. verroxii*
16.	*T. oscarboettgeri* Lindholm, 1929	= *P. t. verroxii*
17.	*C. tentoria albanica* Hewitt, 1933	= *P. t. tentorius*
18.	*C. tentoria tentorioides* Hewitt, 1933	= *P. t. tentorius* × *verroxii*
19.	*C. tentoria piscatella* Hewitt, 1933	= *P. t. tentorius*
20.	*C. tentoria subsulcata* Hewitt, 1933	= *P. t. tentorius*
21.	*C. tentoria karuica* Hewitt, 1933	= *P. t. tentorius* × *verroxii*
22.	*C. tentoria duerdeni* Hewitt, 1933	= *P. t. tentorius* × *verroxii*
23.	*C. tentoria lativittata* Hewitt, 1933	= *P. t. tentorius*
24.	*C. tentoria karuella* Hewitt, 1933	= *P. t. tentorius*
25.	*C. tentoria hexensis* Hewitt, 1933	= *P. t. trimeni*
26.	*C. schonlandi* Hewitt, 1934	= *P. t. verroxii*
27.	*C. fiski cronwrighti* Hewitt, 1934	= *P. t. verroxii*
28.	*C. fiski orangensis* Hewitt, 1934	= *P. t. verroxii*
29.	*C. fiski colesbergensis* Hewitt, 1934	= *P. t. verroxii*
30.	*C. fiski grica* Hewitt, 1934	= *P. t. verroxii*
31.	*C. fiski gricoides* Hewitt, 1934	= *P. t. verroxii*
32.	*C. verroxii amasensis* Hewitt, 1934	= *P. t. verroxii*
33.	*P. depressa* FitzSimons, 1938	= *P. t. verroxii*

[1] Though not a new name, this synonym is included here because of its importance, due to misuse at so early a date (1855).

a moderate sized though slender scute, it is sometimes absent — as in the type of *strauchi* v. Lidth de Jeude and another specimen in Leiden. In such cases of absence the first marginals meet medially, thus seeming to imply that the nuchal has been lost by extreme attenuation.

The scalation of the forelimb differs in the two species (Pl. 7*A*, *B*), but in both there are only a few enlarged scales and many small ones. This is in contrast to the situation in the *tentorius* group where there are more enlarged scales in rather definite rows, and fewer smaller ones.

Though *P. oculifer* has a very extensive range, it seems not to extend south of the Orange River. Boulenger's record of this species from "between Richmond and Victoria West" (questioned by Hewitt:1934) was based on a misidentified *tentorius verroxii*.[1] On the other hand, *geometricus* is, or was — it is now very rare or extinct — confined to a few districts in the vicinity of the Cape Peninsula. Though these are well-marked forms, readily distinguishable on color, shape of nuchal, scalation of forelimb, etc., in view of their geographic separation it is difficult to evaluate the differences in terms of species versus subspecies distinction. It is always possible to claim that these are clinal extremes of a formerly intergradient population. However, since distance has been demonstrated on more than one occasion to mean reproductive isolation, even when morphological difference is not great, and since the two forms are separable on many characters and cannot intergrade in nature, we have conservatively maintained them as full species. In modern systematic terms, however, they certainly belong to one superspecies.

In this connection a further point may be mentioned. North of the Orange River *oculifer* occurs over part of the range of *tentorius verroxii*. Differences beyond sympatric species are commonly used as a measure of the specific distinctness of allied allopatric forms. With this in mind a comparison reveals that the populations of *oculifer* that coexist with the far more variable *t. verroxii*, resemble the latter more than do the more distant *t. tentorius* and *t. trimeni*. Both sympatric populations are relatively dull colored and have large femoral tubercles; neither have high conical vertebrals. Usually *oculifer* has a very serrate

[1] Specimen examined at the British Museum by E.E.W.

margin but sometimes varies towards a non-serrate condition; while *t. verroxii* is normally not serrate, occasionally within the range of *oculifer* it may be strongly serrate (Power:1932b). Also in some specimens of *t. verroxii* the nuchal shield may be rather large, in size and shape approaching the nuchal of *oculifer*. In general the differences between these sympatric species, while perfectly clear-cut, are no stronger than those between *geometricus* and *oculifer*. On this criterion also these two last may be regarded as full species.

The second species group is interpreted by us to consist of a single highly variable species — *tentorius* — of complex population structure. Reference has frequently been made to individual variability among testudinines but — measured by the variation seen within a single small local population — probably no one species exhibits greater variability than does *tentorius*. Two excellent studies of such variation in *tentorius verroxii* have already been published. That of Power (1932b) on a series of 25 from, or near, Niekerks Hope, just north of the Orange River, and another by Lorenz Müller (1939a) on 45 individuals of the same race from Carmel Rust, near Phillipstown. Much further information on variation can be found in Hewitt's several papers, also in Duerden's (1907c) review of the "*geometricus* group." The last two authors have seen far more material than anyone else, and therefore should have had a better general view of both individual and geographical variation, but we must add that each of these authors has, in his own way, diminished the value of his work for subsequent investigators.

Far more unfortunate than Hewitt's peculiar taxonomic concepts are the unsystematic and erratic nature of his descriptions. A great many individual specimens are described in some detail, but the descriptions are not comparable, i.e. do not consistently deal with the same characters; consequently they are not usable by anyone lacking access to his material.

Duerden's fault springs from an opposite prejudice to that of Hewitt — denigration of all local varieties — and with it a tendency to suppress all locality data. Thus in Duerden's paper there are many general statements about variation, but too often these statements are not tied to specimens with specific localities.

Comments such as these on Hewitt's and Duerden's work

would be neither necessary nor appropriate if theirs were not the major works on this whole group, done on the spot and with abundant collections. Although one or both of us have seen much material, including types, in the British Museum, in Leiden, in Frankfurt, Lorenz Müller's series in Munich, cotypes of several of Hewitt's forms in the Museum of Comparative Zoology and certain material generously loaned by the Transvaal Museum, we have not seen all of this material at one time or in one place. Nor have we seen the animals alive, and we are in no position to solve by judicious collecting in critical localities any of the many problems that have become evident to us. It remains an inescapable fact that these tortoises are forms of Southern Africa which are not too profitably studied at a distance of many thousand miles. The complex relationships will be satisfactorily resolved only when South African workers, utilizing all the material available to them, undertake studies of variation as meticulous as those of Power and Lorenz Müller.

Owing to the distance separating us from the principal South African collections, and because of our inability to explore the intricacies of local variation, we have been compelled to take a broad view of the *tentorius* complex. While not fully satisfied with our interpretation, we present the following picture:

In the vicinity of Grahamstown, in southeastern Cape Province, a *Psammobates* population occurs that is characterized by:

(1) high conical vertebrals;

(2) a strongly contrasting dorsal pattern of narrow yellow or orange rays on a dark ground;[1]

(3) a plastral pattern consisting of a dark central figure with sharply defined boundaries that are not broken up by lateral rays, the whole surrounded by a broad yellow border;

(4) the scalation of the forelimb from elbow to wrist, usually with three longitudinal rows of enlarged scales, none of which is conspicuously disparate in size;

(5) hinder side of each thigh with a very large, sharp, subconical tubercle.

In the northwest corner of Cape Province, including western Little Namaqualand near the mouth of the Orange River, and in

[1] However, we figure a specimen (Pl. 10D) in which the relative width of black and yellow rays is reversed. This lighter pattern is still very different from anything that has been observed in other populations.

nearby localities on the slopes behind the high plateau, there is present a second population characterized by:

(1) high conical vertebrals;

(2) a strongly contrasting dorsal pattern of moderately wide yellow or orange rays on a black ground;

(3) a plastral pattern consisting of a dark central figure with sharply defined boundaries broken through by numerous yellow rays, the whole surrounded by a broad yellow border;

(4) the scalation of the forelimb from elbow to wrist without three longitudinal rows of enlarged scales; instead, either a single scale greatly enlarged in relation to the others, or else a single row of especially enlarged scales;

(5) hinder side of each thigh without any very large, sharp, subconical tubercle, though small inconspicuous tubercles may be present.

On the plateau of eastern Little Namaqualand, just east of the last population, is one that differs from both the preceding groups. Its characters are:

(1) vertebrals quite flat, not in the least conical;

(2) a dorsal pattern that is not so strongly contrasting, its rays broader, its coloring duller;

(3) a plastral pattern consisting of a dark central figure, as in the preceding groups, but paler and characterized by the indistinctness of its boundary with the surrounding broad yellow border;

(4) the scalation of the forelimb from elbow to wrist consists of relatively few scales variously enlarged;

(5) hinder side of each thigh with a very large, sharp, subconical tubercle.

These are the three peaks of character differentiation which are to be found within the *tentorius* complex. All three populations share certain characters:

(1) the plastral pattern never covers the entire plastral area, which always has a broad clear border;

(2) usually two axillaries present, sometimes more, rarely one;

(3) the nuchal shield is usually broader than long, frequently minute, occasionally absent, in the latter event the first marginals do not meet.

With these characters uniting them in a species group, what

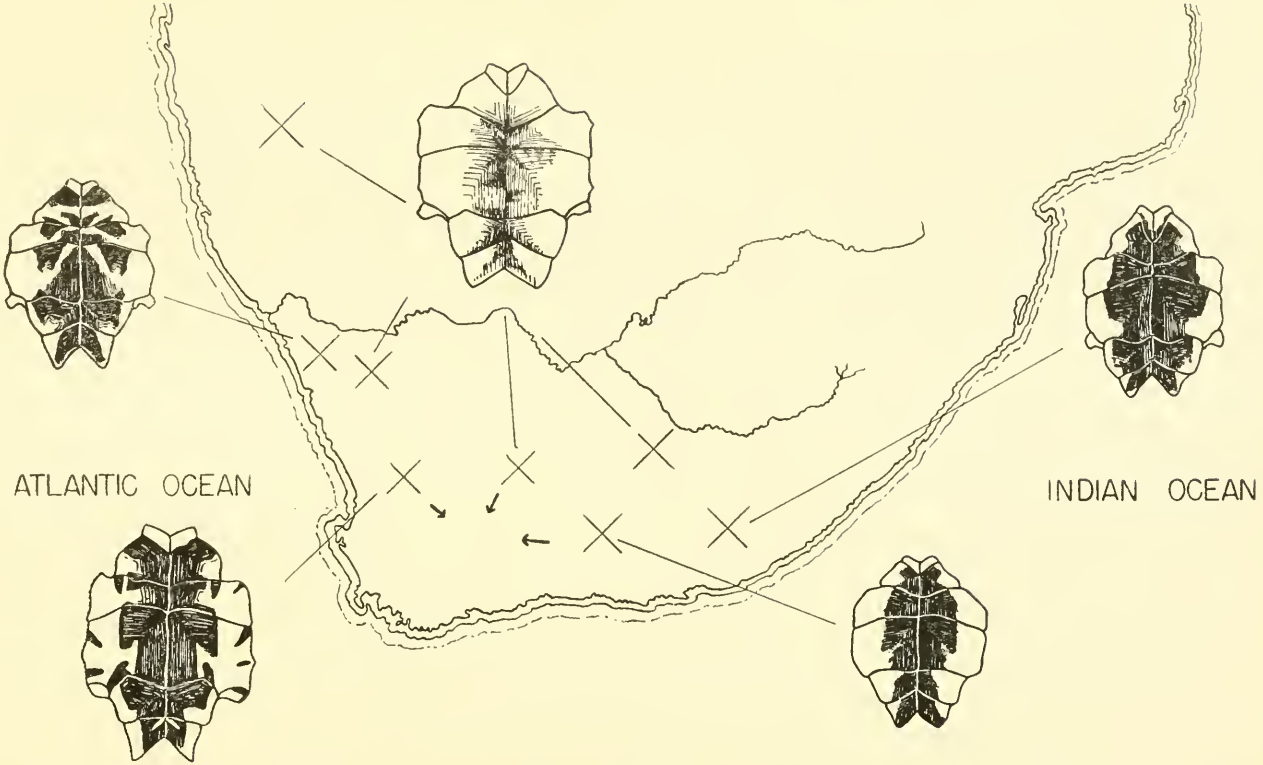


Fig. 28. Distribution of plastral patterns in *Psammobates tentorius*. The area of converging arrows indicates the district in which all types of plastral patterns occur together (see Pl. 11). Plastral patterns drawn from specimens. (P. Washer del.)

do the three populations represent — species, subspecies, or local assemblages unworthy of nomenclatorial recognition?

So far as we are aware no intergradation occurs between the Orange River mouth population and the one on the plateau to the east of that area. In fact, representatives of both populations labeled "Steinkopf" are present in the Museum of Comparative Zoology collection. Hewitt (1934:308-309) has suggested that the populations are probably allopatric; an opinion with which we concur though apparently the evidence is not positive. However, whether the populations overlap or not is relatively unimportant. They are adjacent; they are strikingly different, and they show no sign of interbreeding. In short they are behaving like good species.

But these populations in northwestern and northeastern Little Namaqualand are the only adjacent populations in the *tentorius* complex that are sharply distinct. Everywhere else contiguous populations of the *tentorius* complex merge into one another. Less strongly differentiated populations cluster around the three peaks of difference already described and, wherever they meet, coalesce by rather gradual transitions.

At this point, in order to facilitate ready reference to the concepts involved, we propose applying the available scientific names, using for this purpose topotypical ones that may ultimately be synonymized. Thus *trimeni* Boulenger, whose concept is substantially the same as ours, can be applied to the Orange River mouth population in which the plastral pattern is broken into sharply distinct fragments.

For the moment *schonlandi* Hewitt may be applied to the neighboring population in eastern Little Namaqualand. The precise locality of the ♂ type is unknown, but a ♀ paratype was suspected to have come from O'okiep. The type locality may confidently be restricted to O'okiep as the population of this and surrounding localities is clearly what we understand by *schon-*

landi. Our conception is based on three paratypes from Steinkopf (M.C.Z. 4222-4).

The name *tentoria* Bell may be applied to the population centering around Grahamstown. Here again the type has imprecise locality data, merely "South Africa," but we may with confidence restrict the type locality to Grahamstown, as the type conforms satisfactorily to that population.

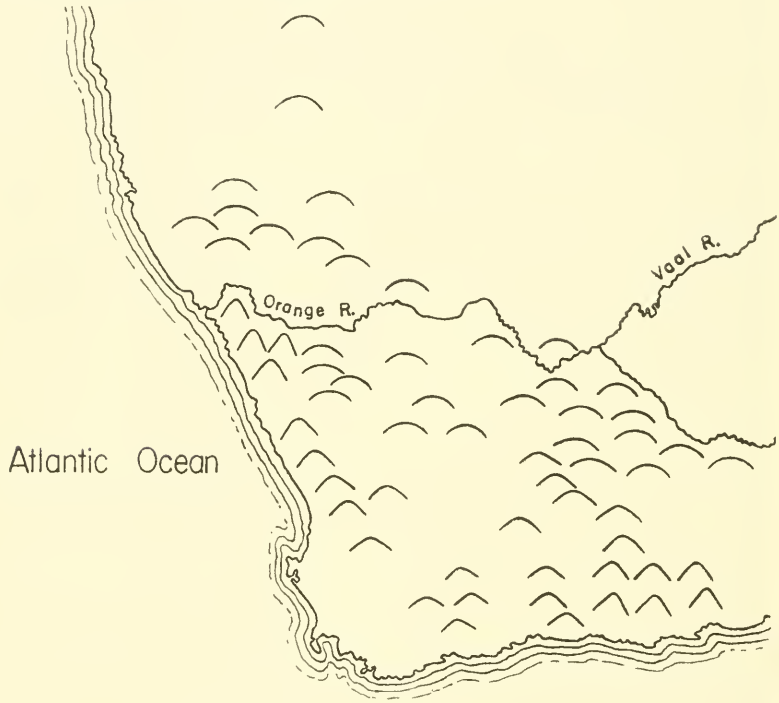


Fig. 29. Distribution of vertebral height in *Psammobates tentorius*. Subjective estimates of average height in the various populations.

(P. Washer del.)

It is now necessary to discuss the populations satellite to those which constitute peaks of difference.

To the south of typical *trimeni* in northeastern Little Namaqualand is a population displaying the characters of *trimeni* in

much reduced intensity. The vertebrals instead of being conical are relatively low. The forelimb no longer possesses any scale that is strikingly larger than its fellows. The dorsal coloration is duller, the rays wider. The plastral pattern is interrupted by yellow rays but is no longer separated transversely. We have an example of this sort from Bitterfontein (M.C.Z. 33451), and have seen others from near Calvinia (T.M. 18258) and Nieuewerust (T.M. 18257). Similuar specimens from Hex River Valley were named *tentoria hexensis* by Hewitt.

To the north and west the typical population of *tentorius* grades into others that possess its characters in an attenuated degree. The vertebrals are less conical; in this character there is a considerable range of variation but it centers about a different and lower mode. The dorsal pattern becomes less sharply defined and may have broader rays. The plastral pattern changes very little but occasionally may be very faint, even though still sharply bounded. Still farther north on the Karroo plateau the populations progressively lose *tentorius* characters and approximate those of *schonlandi*. The vertebrals are only slightly and occasionally raised. The dorsal pattern is very variable but usually broad rayed. The plastral pattern is extraordinarily variable, sometimes almost a faded, vaguely outlined, *tentorius* pattern, or an indefinite rayed pattern, in others just an indistinct central infuscation, or entirely absent.

It is for these populations to the north and northwest of *tentorius* that extreme variability has been recorded by Power and Lorenz Müller. Of them it is said that no one individual is like another, and the amplitude of variation is indeed such that from one locality Boulenger described two full species, while from the same place Hewitt described still a third form; all regarded by us as strict synonyms. These plateau populations appear to be really more variable than typical *trimeni* or typical *tentorius*, their characters only attaining some degree of definition and constancy where. as *schonlandi* Hewitt, their ranges abut on that of *trimeni*.

The variable populations of the Karroo plateau extend north of the Orange River into Great Namaqualand. Here a distinct variant occurs. This is the melanistic unicolored variety named *bergeri* by Lindholm. So far, only single specimens have been re-

corded, viz. the type from Gibeon; another from "Herreroland" (Werner:1910a); a third from Upington in Gordonia district (Siebenrock: 1910). Also referred to *bergeri* by Mertens (1955a: 37) is a specimen without exact locality identified by Sternfeld (1911d:49), and one in his own collection obtained at Klein Windhoek but believed to be an escaped captive not native to the locality. We have also seen a British Museum example from Barby, Tiraz Mountains, Southwest Africa.[1]

Since in each instance these *bergeri* individuals appear to differ from surrounding populations only in color, and their distribution so far as known is quite erratic, we have regarded *bergeri* as merely a color phase occurring in, but nowhere characterizing, the northern populations of the plateau tortoises of this complex. On the other hand, when Mertens (1955a:37) was in Southwest Africa he was told that all the tortoises in one part of Great Namaqualand were of a uniform red-brown color. Such a report requires verification, for of the "*bergeri*" localities only Gibeon and Barby are relatively near one another. Not only is Upington remote from both, but it is separated from them by localities (e.g. Keimoes, Lower Molopo River; Klein Karas Mtns.) in which patterned tortoises occur.

Whether the Great Namaqualand populations allied to *schonlandi* meet *trimeni* on the south, or whether they are separated from the latter by the Orange River, is uncertain. From north of the Orange the only records of *trimeni* worth attention are those of Werner (1910a) and Mertens (1955a). Werner (1910a) presents a photograph of the specimen from Keetmanshoop, but this is too poor to permit of reappraisal. The descriptions and photographs of Mertens (1955a) are more satisfactory and indicate that *trimeni* may really coexist with *schonlandi*-like forms north of the Orange River.[2]

Summarizing the information so far presented, we postulate the following:

[1] The skull of this specimen has been prepared and confirms the assignment to *Psammobates* on three grounds: (1) the characteristic maxillary projection extends on to the roof of the palate; (2) the ventral processes of the vomer are approximated; (3) the anterior palatine foramina are small and inconspicuous.

[2] Dr. Mertens states (in a letter of 19.xii.55) that the plastral patterns of the Southwest African specimens referred by him to *trimeni* (1955a: 36), agree "sehr genau" wih the pattern of the type of *trimeni* as figured by Boulenger.

The northwest form (typical *trimeni*) grades southward into a less distinctive population that approaches more closely the other assemblages of the *tentorius* complex. The southeast form (typical *tentorius*) grades in almost clinal fashion northward and northwestward into populations again less and less like the topotypes and increasingly like a third distinctive group. This third population, nearly or entirely confined to the inland plateau (whereas the other assemblages are more nearly coastal), is over most of its range very variable (to a limited extent geographically, to a much greater extent individually) and is only sharply distinct and relatively uniform where, as *schonlandi,* it meets the northwest population.

Undiscussed so far is the southwest area that the southern population of *trimeni,* and that allied to *schonlandi,* approach from the north, and which the populations of *tentorius* enter from the east. This is the meeting place of all three of the major series of assemblages of the *tentorius* complex, and adjacent to this meeting place the representatives of all three have already lost every distinctive character except plastral pattern. All are relatively dull in color, without very convex vertebrals and with rather uniform forelimb scalation, i.e. three longitudinal rows from elbow to wrist.

Through the courtesy of the Transvaal Museum we have been able to examine a series of nine specimens from Matjesfontein, which is in this critical area. All three types of plastral pattern, as well as intermediates between them, occur in this small sample (Pl. 11).

This then is the picture which has emerged for us as a broad and general view of the *tentorius* complex. It remains to be considered how this situation is to be interpreted biologically and treated taxonomically.

Despite the lack of any evidence of introgression or intergradation between typical *trimeni* and adjacent "*schonlandi,*" the *tentorius* complex taken as a whole appears to be a reproductive unit. By the indirect route of a chain of allopatric populations which appear to interbreed freely at their points of contact, it seems clear that even *trimeni* and "*schonlandi*" must be able to exchange genes. We may, therefore, consider that the whole complex constitutes one species for which the name *Psammobates*

tentorius (Bell) is available. The question arises as to whether this species should be subdivided; if so, how minutely?

The problem of species subdivision is only partly a biological one. To describe the biological situation completely would require a far more elaborate analysis than that provided above and a knowledge that no one now possesses. No series of names can prove a satisfactory substitute for such a biological description. If it is admitted that names cannot tell the full story, is there any use or purpose in applying subspecific names?

We believe that the three well-differentiated centers or peaks already described, around which other populations cluster, merit recognition, especially in view of the fact that two of them behave toward one another as if they had already reached the specific level. By granting these populations names we are endeavoring to indicate something both in regard to their past and to their potential history. We believe that the typical populations of *trimeni, "schonlandi,"* and *tentorius,* represent the focal *loci* of the *tentorius* complex during a previous fragmentation of its range; that during this former separation these three populations built up the system of features that now distinguish them as peaks of difference within the complex. In terms of characters they are even now almost at the specific level, but the satellite populations surrounding them — showing as they do every apparent evidence of intergradation — testify that reproductive isolation has not been achieved. Still the process of differentiation has gone so far that we may rather confidently assert that if fragmentation and isolation again occurred, these populations showing peaks of difference are the best candidates to pass the species threshold. As true "incipient species," we believe they may legitimately receive names.

Our subspecies are to be conceived of primarily in terms of the peaks of difference — the three topotypical populations of *trimeni, "schonlandi,"* and *tentorius.* Simply for convenience in demarcating subspecific boundaries, we attach to each of these central populations its satellite groups, without granting any of these separate nomenclatorial recognition. We agree with Hewitt that each of these satellite local populations may be recognized by modal tendencies, though probably not by any constant feature, but we also think that, without extreme artificiality, it will never be possible to set limits to these populations. To ac-

cept or erect names for these local groups would be to multiply boundaries that, by reason of intergradation, are vague at every level.

We have chosen to recognize only three somewhat arbitrary ranges which are based on the convenient character of plastral pattern. All populations possessed of a plastral pattern that is sharply bounded, but indented or broken through by a series of

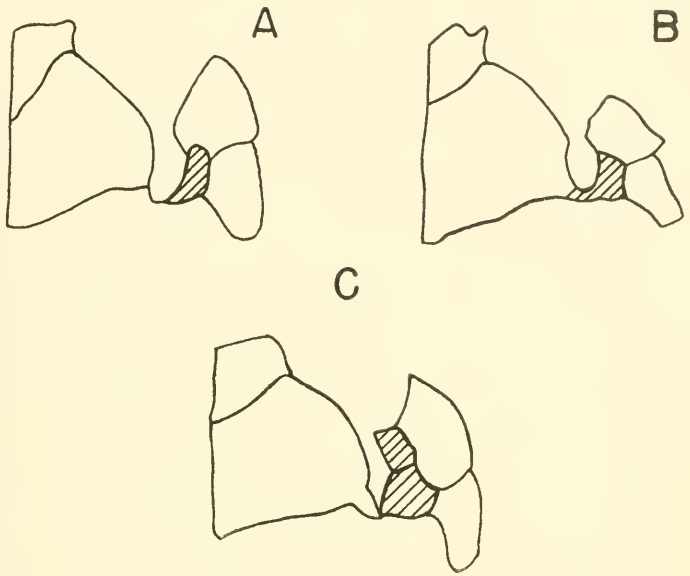


Fig. 30. Axillaries in various species of *Psammobates*. *A*, *P. geometricus* (M.C.Z. 32184); *B*, *P. oculifer* (M.C.Z. 42158); *C*, *P. t. verroxii* (M.C.Z. 42224).

(P. Washer del.)

yellow rays, we assign to *trimeni*. All populations possessed of a plastral pattern sharply bounded, but very little indented or quite intact, we refer to *tentorius*. All populations with a plastral pattern that is both indistinct and variable, we group under the name *verroxii* A. Smith which antedates *schonlandi* Hewitt. The population around Matjesfontein we cannot allocate since it comes from an area of intergradation between all three forms.

We have felt that the complex geographical variation of these forms was a phenomenon meriting rather full discussion and, indeed, further investigation. It may be noted that during this discussion we have arrived at substantially the same taxonomic allocations proposed by Duerden in 1907. It is hoped that by dealing with the problem of geographic variation more elaborately than he did, the conclusions are placed on a firmer footing.

Key to the Species and Subspecies of Psammobates

1. Plastral pattern dark brown or yellow brown, highly ornate, covering entire plastral area; anterior and posterior margins of carapace typically *very* sharply serrate, even spinose; nuchal large, usually subtriangular; axillary single, normally fused with humeral; forelimb with a few large scales on its anterior surface. Range: north of the Orange River, viz. Southwest Africa; Beehuanaland; Transvaal; Orange Free State; and Griqualand West in Cape Province ..... *oculifer* (Kuhl) (p. 315)

   Plastral pattern, if covering entire plastral area, black on yellow, otherwise restricted to central area of plastron or absent; anterior and posterior margins of carapace typically *not* sharply serrate, never spinose; nuchal, if present, smaller, either elongate or broad; axillaries 1 or 2, not united with the humeral; forelimb with variable scaling anteriorly 2

2. Plastral pattern never absent, black on yellow; margins of the plastral shields, even laterally and on the bridge, either wholly black or black broken by yellow rays; nuchal very variable in size but typically elongate, occasionally absent; axillary 1; forelimb anteriorly with a few large scales which are *not in contact* but separated by smaller ones. Range: extreme southwest Cape Province within a 100 mile radius north and east of Cape Town..*geometricus* (Linnaeus) (p. 319)

   Plastral pattern sometimes absent, otherwise black or brown and yellow, peripherally a more or less broad zone of yellow that is usually *entirely devoid of markings;* nuchal very variable in size but typically broader than long, often minute, rarely absent; axillaries 2 or 3, rarely 1; forelimb anteriorly with large juxtaposed scales, not separated by smaller ones 3

3. Plastral pattern, when present, without a well defined outline; dorsal shields never strongly conical. Range: Orange Free State (possibly) and northern Cape Province north through Southwest Africa, occurring mostly at elevations above 3000 feet....*t. verroxii* (A. Smith) (p. 324)

   Plastral pattern with a well defined outline; dorsal shields more or less strongly conical; occurring mostly at elevations below 3000 feet.... 4

4. Plastral pattern broken through by light rays and/or its outline indented by a series of encroachments of the pale ground color. Range: Cape Province (Little Namaqualand south to near Touw's River) north to Southwest Africa (Keetmanshoop, the only record) .....
t. trimeni (Boulenger) (p. 333)

Plastral pattern without light rays crossing and with few or no indentations. Range: Cape Province (mostly south of 33° parallel) from vicinity of Fish River west to beyond Uniondale and Willowmore
t. tentorius (Bell) (p. 336)

Psammobates oculifer (Kuhl)

1820. *Testudo oculifera* Kuhl, Beitr. Zool. Anat., p. 77: Cape.
1831c. Gray, 22.
1865. Strauch, 61.
1889a. Boulenger (part), 165 (omit specimen Richmond to Victoria West).
1890. Strauch, 54.
1893a. Boettger, 10.
1897. Siebenrock, 247.
1898. Sclater, W. L., 97.
1898. Siebenrock, 425.
1899. Siebenrock, 566.
1901. Lampe, 192.
1902a. Werner, 341.
1904c. Siebenrock, 307.
1907a. Duerden, 9.
1907b. Duerden, 76, pl. viii, fig. 12.
1907c. Duerden, 196.
1909a. Siebenrock, 524.
1910. Siebenrock, 704.
1910a. Werner, 301.
1911. Lampe, 147.
1911b. Sternfeld, 409.
1911d. Sternfeld, 49, fig. 61.
1912b. Werner, 434, pl. —.
1914a. Hewitt, 247.
1929. Flower, 31.
1931. Hewitt, 499.
1931. Power, 44.
1932b. Power, 467.
1934a. Mertens and Müller *in* Rust, 9.
1935b. FitzSimons, 304.

1937b. Mertens, 5.
1939a. Müller, L., 129, pl. xi, fig. 7.
1950. Williams, 550, 551.
1955a. Mertens, 34, pl. iii, figs. 7-8.
1839. *Testudo semiserrata* A. Smith, Ill. Zool. S. Africa, Rept., pl. vi aa: "between Latakoo and the Tropic of Capricorn."
1844. Gray, 8.
1851. Duméril and Duméril, 3.
1855. Gray, 9.
1880c. Vaillant, 25.
1886b. Boulenger, 542.
1887b. Boettger, 138.
1844. *Emys oculifera* Gray, 28.
1862a. *Clemmys oculifera* Strauch, 32.
1870c. *Peltastes semiserratus* Gray, 656.
1870e. Gray, 9.
1872c. Gray, 5.
1873b. Gray, 10.
1893a. *Homopus signatus* Boettger (part), 8 (juv. ex. "Namaland").
1894a. Boettger, 88.
1894. Fleck, 83.
1933b. *Chersinella oculifera* Hewitt, 263.
1934. Hewitt, 337.
1935a. FitzSimons, 520.
1937a. *Psammobates oculifera* (*sic*) Hewitt, 791, fig. 2.
1938. *Testudo geometrica* Schepers (not of Linnaeus), 535-555, figs. 1-5.
1939. Schepers, 451-495, 1-8.
1948a. Schepers, 9-11, figs. 1-4.
1948b. Schepers, 1-212, figs. 1-250.

A further citation of "*oculifera*" will be found under *Psammobates tentorius verroxii*.

Common names. Serrated Tortoise (preferred); Toothed Cape Tortoise (Gray:1844); Kuhl's Tortoise (Flower:1929).

Illustrations. Excellent figures (lateral and plastral views) copied as our Plate 7 are furnished by Sir Andrew Smith (1839:pl. vi), who contrasts the nuchal and forelimb (figs. aa) with those of *geometricus* (figs. bb). Siebenrock (1910) shows the carapace and plastron of a hatchling. Sternfeld (1911d:fig. 61) provides a sketch of the buttock tubercle. Werner (1912b) has a colored plate of both adult and juvenile.

Types. The principal discussions on the status of this species and its synonym have been by Strauch (1865; 1890), Boulenger

(1889a), Duerden (1907c), and Siebenrock (1940c; 1910).

Description. Beak more or less strongly hooked, tricuspid, edge of jaws more or less serrate; prefrontal divided longitudinally or broken up; frontal broken up; upper head shields small, irregular; forelimb anteriorly with a few unequal (one extremely large) tubercular scutes (but area distal to the largest formed of small scales), forming 2-4 longitudinal and 4-6 transverse series from elbow to outer claw; claws 5; hinder side of thigh with a large, and occasionally a few subsidiary, subconical tubercles; heel with or without [1] conical, spurlike tubercles; tail in both sexes devoid of tubercles on sides and without a terminal claw-like tubercle.

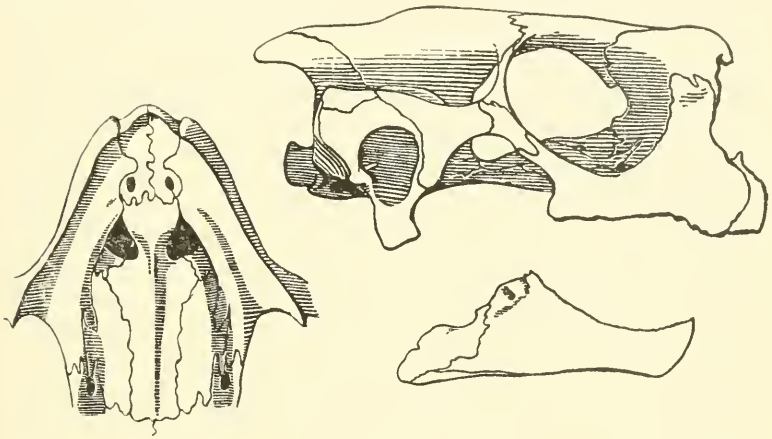


Fig. 31. Skull of *Psammobates oculifer* (A.M.N.H. 7094). Condylobasal length 23 mm.

(S. McDowell del.)

Carapace convex, sides descending abruptly, shallowly notched in nuchal region, anterior and posterior margins more or less expanded, sometimes reverted, and strongly (rarely weakly) serrated; dorsal shields concentrically striated; nuchal present, usually large, subtriangular, more or less projecting into nuchal notch; vertebrals 5, rarely 4, 6, or 7,[2] more or less swollen,

[1] Both present and absent in United States National Museum material.

[2] Four in a tortoise from Kooa (*fide* Werner :1910a); 6 in Keetmanshoop specimen; 7 in one (U.S.N.M. 63021) from Bechuanaland.

typically *not* conical, broader than long, about as broad as, or broader than, or narrower than, the costals; costals 4, not forming an angle with the lateral marginals; marginals 11, rarely 10 or 12; supracaudal undivided, incurved in ♂♂, downwardly directed in ♀♀.

Front lobe of plastron anteriorly more or less produced and openly notched; gulars paired; pectorals narrow where they meet, sometimes even separated,[1] their anterior border sloping towards the axillary notch; axillary 1, almost always fused with the humeral; inguinal moderate, meeting femoral;[2] hind lobe deeply notched posteriorly.

Plastral formula: Abd>h>(g, f, an)>p; g usually>an, though sometimes=or<.

Color. Carapace brownish yellow or horn color (♂), with a very variable pattern of dark brown or black rays of more or less equal width, numbering 6-10 on the vertebrals and costals. Plastron yellowish with light or dark brown (black, *fide* Gray: 1844) rays.

For lengthy discussion of ontogenetic changes in coloration see Siebenrock (1910); for detailed individual variations Hewitt (1933b) and FitzSimons (1935b).

Size. Carapace length of a ♂ (T.M. 15999) from near Kimberly, 118 mm., breadth 82 mm., height 61 mm. Carapace length of a ♀ (T.M. 15998) taken with above, 133 mm., breadth 99 mm., height 70 mm. (FitzSimons:1935a).

Sexual dimorphism. Siebenrock (1910) states that in ♂♂ the vertebrals are flatter than in the ♀♀, but our meagre material scarcely bears this out. However, Siebenrock is correct in stating that the ♀ carapace is relatively higher than that of the ♂. Unlike most species, according to Hewitt (1933b), there is no disparity in size between the sexes.

Breeding. On November 29, 1933, a pair were engaged in courtship on the Kimberly to Schmidtsdrift road, the ♂ scuttling around the ♀, butting against her shell, and periodically emitting short, low, grunting coughs. Though approached closely by FitzSimons (1935a), the ♂ only ceased his activities when actually picked up.

[1] As in the type and a Waterberg tortoise (M.C.Z. 42158).

[2] Except in a Quickborn specimen mentioned by Hewitt (1931).

The egg of a Kimberly tortoise measured 31 x 39.5 mm (Hewitt:1934).

Enemies. Jackals, ratels and the brown hyena will all break open the plastron to get at these tortoises (R. D. Bradfield in Hewitt:1934); Bataleur Eagles also prey upon them according to the Hereros (Hewitt:1934).

Habitat. Frequents sandy plains and grassgrown flats (Power: 1931; 1932b); grassland savannas of the inland plateaus according to Bradfield (in Hewitt:1933b).

Localities. Bechuanaland: Gemsbok; *Gomodimo; *Kalahari; Kamelslip; Kaotwe; Kooa; Lake Ngami; Lehututu (as Lekutu) to Kang; Makarikari; Mookane (Moocane); Palapye Road; *Serowe (U.S.N.M.); Vlei Topan. *Transvaal:* Jamestown; Linokana. *Orange Free State:* Bothaville; Modder River. *Cape Province:* as "Cape" (type locality); Danielskuil (Daniel's Kuil); *Kimberly; Kuruman; "Latakoo to Tropic of Capricorn" (type locality of *semiserrata*); Niekerkshoop (Niekerk's Hope); Schmidtsdrift to Kimberly; Saint Clair; Douglas; Warrenton; Witput Siding; Zoetvlei near Vryburg. *Southwest Africa:* Aukeikas, 25 km. west of Windhoek; Aus (Auas; Oas); *Etosha Pan-near; *Gaucha (U.S.N.M.); Gibeon; Gobabis; Grootfontein; *Nama (U.S.N.M.); Ogosongomingo to Great Waterberg; Omaruru; Ondonga; Quickborn Farm, Okahandja; Rehoboth; Rietmond; Sandup; Swakopmund; *Waterberg; Windhoek (Windhuk).

Range. Extreme western Transvaal and western Orange Free State northwest through Bechuanaland and Southwest Africa almost to the frontier of Angola.

Clanwilliam, we believe, was not the true source of the specimen but the donor's address cited by Duerden (1907a). It is probably responsible for Little Namaqualand being included in the range by FitzSimons (1935b:305) and Mertens (1955:35).

Psammobates geometricus (Linnaeus)

1734. *Testudo minor, amboinensis* Seba, Rerum Naturalium Thesauri . . . 2, p. 130, pl. lxxx, fig. 8: "Amboina" (in error).

1758. *Testudo geometrica* Linnaeus, Syst. Nat., ed. 10, 1, p. 199: "Asia" (in error).

1766. Linnaeus, 353.

1784. Daubenton, 628.
1788. Lacépède, 157, pl. ix and Synopsis.
1789. Bonnaterre, 24, pl. vi, fig. 1.
1792. Schoepff, 55, pl. x.
1793. Schoepff, 49, pl. x.
1797. Shaw and Nodder, pl. cccvi.
1802b. Daudin, 260, pl. xxv, fig. 1.
1802. Shaw, 20, pl. ii.
1812. Schweigger, 325, 424 (omit non-African localities).
1814. Schweigger, 56.
1828. Bory de Saint Vincent, 73 (omit Asia occidentale).
1831. Griffith, 10, 54.
1831b. Gray, 5.
1831c. Gray, 12.
1835. Duméril and Bibron, 57.
1835. Temminck and Schlegel (part), 73.
1836. Bell, text, col. pl.
1838. Cuvier, pl. i.
1844. Gray, 8.
1845b. Rüppell, 297.
1849. Smith, A., App., 1, pl. vi, bb only.
1855. Gray (part), 8.
1857. Jan, 35.
1862a. Strauch, 74.
1865. Strauch, 19.
1867a. Steindachner, 3.
1872b. Gray, 3, *in* Sowerby and Lear, pl. xiii.
1882a. Müller, F., 165.
1882a. Peters, 3.
1884a. Rochebrune, 12 (in error).
1886b. Boulenger, 541.
1889a. Boulenger, 162.
1890. Strauch, 56.
1893a. Boettger, 10.
1893. Trimen, 79.
1896. Lönnberg, 11.
1898. Jeude, 4.
1898. Johnston, 361.
1898. Sclater, W. L., 96.
1901. Lampe, 192.
1904c. Siebenrock, 309 (key).
1907c. Duerden, 195.
1909a. Siebenrock, 524.

1910. Siebenrock, 702.
1911. Lampe, 146.
1911d. Sternfeld, 49.
1914a. Hewitt, 247.
1929. Flower, 30.
1929. Rose, 189.
1934a. Mertens and Müller *in* Rust, 9.
1938. Bernstein, 327 (det. doubtful).
1939a. Müller, L., 129.
1954. Noël-Hume, 74.
1767. *Tortue* Knorr, 127, pl. iii, fig. 3 (clearly *geometricus* from this fine colored figure).
1802b. *Testudo luteola* Daudin, Hist. Nat. Rept., **2**, p. 277, pl. xxv, fig. 3: (purchased in Dieppe) No locality.
1820. *Chersine geometrica* Merrem, 32.
1829. Gravenhorst, 20.
1843. *Psammobates geometricus* Fitzinger, 29.
1861. Fitzinger, 411.
1844. *Testudo geometrica* var. *tentoria* Gray (not of Bell), 8.
1855. Gray, 8.
1869c. *Peltastes geographicus* Gray (lapsus: *fide* Gray), 173.
1870c. *Peltastes geometricus* Gray, 655, pl. xiii.
1870e. Gray, 9.
1873b. Gray, 8.
1893. *Testudo Strauchi* Lidth de Jeude, Notes Leyden Mus., **15**, p. 312, pl. ix: Cape of Good Hope.
1907c. Duerden, 201.
1909a. Siebenrock, 523.
1934a. Mertens and Müller *in* Rust, 9.
1933b. *Chersinella geometrica* Hewitt, 260, pl. xiv, figs. 1-7.
1934. Hewitt, 336.
1933b. *Chersinella strauchi* Hewitt, 262.

Further citations of "*geometrica*" will be found under *oculifer, t. tentorius* and *Kinixys b. belliana.*

Common Names. Geometric Tortoise (Lacépède); seerpootjies (*fide* Peers in Hewitt:1934:336).

Illustrations. For a side and plastral view in color cf. Schoepff (1792:pl. x). A. Smith (1839:pl. vi, bb) contrasts the forelimb and nuchal with those of *oculifer.* Photographs of variants are furnished by Hewitt (1933b:pl. xiv, figs. 1-7).

Types. Testudo luteola was synonymized with *geometricus* by Gray (1831b), a disposition with which we are in accord. Lidth

de Jeude separated *strauchi* (still in Leiden Museum where it has been studied by one of us — E.E.W.) because it lacked a nuchal and on the proportions of its gulars, characters that are demonstrably inconstant. It was synonymized with *geometricus* by Duerden (1906), and there seems no justification for its revival by Siebenrock (1909; 1910) and Hewitt (1933b).

Description. Beak moderately or strongly hooked; prefrontal divided longitudinally or broken up; frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few large, unequal, scattered tubercular scutes, forming 6-7 longitudinal and 7-10 transverse series from elbow to outer claw; claws 5; hinder side of thigh without large conical tubercles; tail in both sexes devoid of tubercles on sides and without a terminal clawlike tubercle.

Carapace very convex, sides descending abruptly, deeply notched in nuchal region, posterior margins not or but weakly expanded, slightly reverted, and but rarerly serrated; dorsal shields concentrically striated; nuchal present, typically elongate, occasionally triangular, sometimes minute, rarely absent, when present more or less projecting into nuchal notch; vertebrals 5, rarely 4 or 6,[1] sometimes swollen as truncate pyramids, much broader than long, as broad as, or broader than, or narrower than, the costals; costals 4, rarely 5, usually not forming an appreciable angle with the lateral marginals; marginals 11 or 12; supracaudal undivided, more or less incurved in both sexes.

Front lobe of plastron anteriorly truncate, not or but slightly produced and very shallowly notched; gulars paired; pectorals broadly in contact, their anterior border sloping towards the axillary notch; axillary 1, small; inguinal moderate, meeting femoral; hind lobe deeply notched posteriorly.

Plastral formula: Abd>g>or<h>or=f>or=an>or=p; f usually>an.

Color. Carapace with yellow areolae from which radiate yellow rays (8-15 on vertebrals, 9-12 on costals, 2-4 on marginals) separated by black. Plastron yellow with more or less ill-defined black rays and bands.

The juvenile coloring is substantially the same as that of the adult, according to Siebenrock (1910); however, hatchlings in

[1] Six in figure on plate of Shaw and Nodder (1797).

the Paris Museum seen by E. E. W. possess the *lutcola* pattern (cf. Plate 8A, B).

Size. Carapace length allegedly attains to 240 mm. (*fide* Duerden:1907c); one of 135 mm. is mentioned by Strauch (1862a) with a breadth of 95 mm., and height of 76 mm. Carapace length of type ♀ of *strauchi* was 140 mm.

If correctly identified, a specimen recorded by Daudin (1802b) far surpasses all recent records. In *French inches* it is said to have a length (possibly over the curve ?) of 10″ 6‴=283.6 mm.
breadth ..... 8″ =208.5 mm.
height ..... 3″ 9‴=101.5 mm.

Breeding. Twelve to fifteen eggs are laid according to Bruyere (Lacépède:1788).

Enemies. In all probability mankind is responsible for the extermination, or near extermination, of this handsome little species. Writing of his journey into Caffraria in 1772, the botanist C. P. Thunberg made the following observations.

"Instead of China-vessels and calabashes, poverty had taught them [the Hottentots] to use the shells of the tortoises, which frequent the bushes in the sandy plains, particularly the *Testudo minuta* and *geometrica*" (1795:**1**:182).

"The *Testudo Geometrica* was known here (vicinity of the Cape) by the appellation of the *Syren* (*Syrentie*). This land-tortoise, which probably is the most beautiful of its kind, was found very common in the sandy downs among the bushes. The shells of such as were very small, and consequently the most beautiful, were used for making snuff boxes" (1795:**1**: 243).

"Some of the women . . . had a tortoise-shell hanging at their backs, in which they preserved either their tobacco or bucku (*diosma*). For want of clay tobacco-pipes they use wooden ones" (1795:**1**:194).

"Some of them [Kaffirs] wore about their necks a necklace made of small shells, called serpents skulls (*Cypraea moneta*) strung upon a string, and to this hung a tortoise-shell, for keeping the bukku ointment in" (1795:**2**:82).

"Among their [Hottentots] ointments they mix the powder of a strong smelling herb, which they call Bucku (a species of *Diosma,* frequently the *Pulehella*), and which gives them so

disagreeable, so fetid, and at the same time so rank an odour, that I sometimes could not bear the smell of the Hottentots that drove my wagon" (1795:**2:**187).

Localities. Cape Province: Cape Peninsula; Ceres; Darling; Eendekuil (as Eendekind) district; Klapmuts; Moorreesburg district; Porterville district; Riebeeck Kasteel. (Williston — as Amandelbom Mission on Zak River—we reject on the grounds that it is too far west, and because other species recorded from the mission lead us to suspect it was merely a collecting center for shells brought in by pupils).

Range. Cape Province (Tulbagh, Paarl and Malmesbury districts of the extreme southwest, in former times possibly extending to the Cape Peninsula).

Reported in error from Ascension Id. and Madagascar (Lacépède:1788); Mauritius (Gray:1855); Mozambique (Bianconi: 1851); Nyasaland (Johnston:1898); Great Namaqualand (Sternfeld:1911b) and Senegambia (Rochebrune:1884a).

Psammobates tentorius verroxii (Smith)

1839. *Testudo verroxii* A. Smith, Ill. Zool. S. Africa, Rept., pl. viii: Near the sources of the Orange River (probably in Cape Province, rather than in Basutoland where it has not been taken. See remarks under *Type*).
1844. Gray, 9.
1855. Gray, 8.
1909a. Siebenrock, 525.
1910. Siebenrock, 710 (but Transvaal locality erroneous).
1910a. Werner, 302, pl. x, figs. 15a-b, 16a-b.
1911d. Sternfeld, 50, fig. 62.
1915. Werner, 330.
1934a. Mertens and Müller *in* Rust, 9.
1939a. Muller, L., 129, pls. x-xi.
1870c. *Peltastes verreauxii* (editor's emendation) Gray, 656.
1870e. *Peltastes verroxii* Gray, 9.
1872c. Gray, 5.
1873b. Gray, 10.
1884a. *Testudo verreauxii* Rochebrune (in error), 13.
1886b. Boulenger, 541.
1887b. Boettger, 139.
1889. Boettger, 282.

1889a. Boulenger, 163.
1892. Müller, 214.
1893a. Boettger, 10.
1895. Oudemans, 323.
1904c. Siebenrock, 313, pl. iv and v, fig. 5.
1907c. Duerden, 198.
1911. Lampe, 146.
1914a. Hewitt, 247.
1932b. Power, 466.
1933a. Power, 211.

1886b. *Testudo smithi* Boulenger, Proc. Zool. Soc. London, p. 542: South Africa.
1889. Boettger, 285.
1889a. Boulenger, 165, pl. iv.
1892. Müller, 215.
1893a. Boettger, 10.
1894a. Boettger, 88.
1894. Fleck, 83.
1898. Sclater, W. L., 97.
1904c. Siebenrock, 318, pl. iii.
1904b. Tornier, 304, figs. 12, 14, 15.
1907c. Duerden, 200.
1909a. Siebenrock, 526.
1910. Siebenrock, 712.
1911. Lampe, 147.
1911b. Sternfeld, 410.
1911d. Sternfeld, 50.
1915. Werner, 330.
1934a. Mertens and Müller *in* Rust, 9.

1886b. *Testudo fiski* Boulenger, Proc. Zool. Soc. London, p. 542, col. pl. lviii: De Aar, near Hopetown, Cape Province.
1889a. Boulenger, 165.
1898. Sclater, W. L., 97.
1904c. Siebenrock, 322, pl. v, fig. 6.
1907a. Duerden, 10.
1907c. Duerden, 200.
1909a. Siebenrock, 527.
1910. Siebenrock, 716.
1929. Flower, 31.
1933a. Power, 214.
1934a. Mertens and Müller *in* Rust, 9.
1939a. Müller, L., 129, pl. ii, fig. 1.

1889. *Testudo tentoria* Boettger (not of Bell), 284.

1893a. Boettger, 10.
1894a. Boettger, 88.
1894. Fleck, 83.
1903c. Boulenger, 217.
1889a. *Testudo oculifera* Boulenger (part: not of Kuhl), 166 (specimen ex Richmond to Victoria West).
1903c. *Testudo Seimundi* Boulenger, Ann. Mag. Nat. Hist. (7), **12**, p. 216, pl. xvii: Three miles east of Deelfontein, Cape Province.
1907c. Duerden, 201.
1909a. Siebenrock, 527.
1934a. Mertens and Müller *in* Rust, 9.
1904b. *Testudo boettgeri* Siebenrock (not of Mojsisovics), Anz. Akad. Wiss. Wien, **41**, p. 194: Great Namaqualand, Southwest Africa.
1904c. Siebenrock, 310, pls. i-ii.
1907c. Duerden, 202.
1909a. Siebenrock, 525.
1911d. Sternfeld, 49.
1922a. Mertens, 168.
1906. *Homopus bergeri* Lindholm,[1] Jahrb. Ver. Nat. Wiesbaden, **59**, p. 348: Gibeon, Southwest Africa.
1907b. *Testudo tentoria* var. *fiskii* Duerden (part), 88 (fig. is of *tentoria trimeni*).
1909b. *Testudo bergeri* Siebenrock, 623.
1910. Siebenrock, 713, pls. ii and iv.
1910a. Werner, 304, pl. ix, figs. 14a-c.
1911. Lampe, 146.
1911d. Sternfeld, 50.
1929. *Testudo oscarboettgeri* Lindholm, Zool. Anz., **81**, p. 295; n.n. for *boettgeri* Siebenrock, preoccupied.
1934a. Mertens and Müller *in* Rust, 9.
1934. *Chersinella schonlandi* Hewitt, Ann. Natal Mus., **7**, p. 303, pl. xvi, figs. 46-50: Little Namaqualand, Cape Province.
1934. *Chersinella fiski* Hewitt, 309, pl. xvi, figs. 51-56.
1934. *Chersinella fiski seimundi* Hewitt, 314, pl. xvi, fig. 57.
1934. *Chersinella fiski cronwrighti* Hewitt, Ann. Natal Mus., **7**, p. 317, pl. xvi, fig. 58: Hanover, Cape Province.
1934. *Chersinella fiski orangensis* Hewitt, Ann. Natal Mus., **7**, p. 319, pl. xvi, figs. 59-60: Between Phillipstown and Petrusville District, Cape Province.
1934. *Chersinella fiski colesbergensis* Hewitt, Ann. Natal Mus., **7**, p. 321, pl. xvi, figs. 61-62: Colesberg, Cape Province.

[1] Erroneously synonymized with *Homopus boulengeri* by Siebenrock (1909: 515), who later (1910) correctly assigned it to the *geometricus* group.

1934. *Chersinella fiski grica* Hewitt, Ann. Natal Mus., **7**, p. 323, pl. xvi, figs. 63-66; pl. xvii, figs. 67-71: Marydale, Prieska District, Cape Province.
1934. *Chersinella fiski gricoides* Hewitt, Ann. Natal Mus., **7**, p. 326, pl. xvii, figs. 72-75: Niekerks Hope (= Niekerkshoop), Hay District, Cape Province.
1934. *Chersinella verroxii* Hewitt, 328, pl. xvii, fig. 78.
1937a. FitzSimons, 260.
1934. *Chersinella verroxii smithi* Hewitt, 331, pl. xvii, figs. 76-77.
1934. *Chersinella verroxii boettgeri* Hewitt, 333.
1934. *Chersinella verroxii amasensis* Hewitt, Ann. Natal Mus., **7**, p. 333: Ukamas District, Cape Province.
1934. *Chersinella verroxii bergeri* Hewitt, 335.
1935a. *Chersinella boettgeri* FitzSimons, 520.
1935a. *Chersinella fiskii* ? FitzSimons, 520.
1937e. *Psammobates fiski colesbergensis* Hewitt, 8, pl. iii, fig. 6.
1937e. *Psammobates fiski cronwrighti* Hewitt, 9, pl. iii, fig. 5.
1938. *Psammobates depressa* FitzSimons, Ann. Transvaal Mus., **19**, p. 154, pl. ii, figs. 1-4; pl. iii, figs. 1-2: Aus, Southwest Africa.
1938. *Psammobates fiskii* FitzSimons, 155.
1946a. *Psammobates fiskii fiskii* FitzSimons, 354.
1955a. *Testudo verroxii bergeri* Mertens, 37, pl. iv, fig. 12.

Further citations of "*verreauxi*" will be found under *t. tentorius*, and "*fiski*" under *t. trimeni*.

Common name. Northern Tent-Tortoise (would seem to be the most descriptive).

Illustrations. Excellent figures (lateral and plastral views; nuchal and forelimb) of the type have been furnished by Smith (1839:pl. viii). Siebenrock (1904c:pls. i-v) supplies good photographs of *verroxii, smithi, fiski* and *boettgeri* (type), and Hewitt (1934:pls. xvi-xvii) of the types of his numerous subspecies. More recently Müller (1939a:pls. x-xi) has photographed many extremes of this highly variable form.

Types. The type of *verroxii* has been definitely identified by FitzSimons (1937a:260) as a stuffed specimen, now minus eleven shields, in the Royal Scottish Museum at Edinburgh.

As to the type locality of *verroxii*, Power states (1932b:466) that he has systematically searched Sir Andrew Smith's works from which "it appears that he did a great deal of collecting in that part of the country at present occupied by the divisions of Bethulie, Smithfield, and Rouxville." Power concludes that

the type "was taken somewhere north of Aliwal North, between the Orange and Caledon Rivers; that is to say, roughly 260 miles east of Niekerk's Hope."

Dr. V. FitzSimons, writing us on 12.v.54, considers Power's suggestion regarding the type locality as reasonable, adding that he has never seen any *verroxii* in the eastern Orange Free State. Mr. C. Jacot-Guillarmod, a keen naturalist whom we also consulted, replied that the few tortoises seen by him in the Orange Free State appeared to be referable to *Homopus*.

Writing on 1.ix.54 from Mamathes, Basutoland, Mr. Jacot-Guillarmod says: "I looked up Andrew Smith's itinerary and find that the type locality of the tortoise cannot be far from here. I should say just north of here round about Levibe, Ficksburg, or even east of here, perhaps along the Phuthiatsana River as he went up this river to its source. This means that he passed within four or five miles of Mamathes."

However, though "the sources of the Orange River" are in Basutoland, where Mr. Jacot-Guillarmod has been residing for the past 36 years, he tells us that during all that time he has never seen a tortoise in the Protectorate. Even the leopard tortoise can no longer be found, and if *verroxii* ever did occur it has presumably been exterminated for tortoises are highly prized by the witch-doctors.

Hewitt (1933b) believes that *verroxii* may be distinguished from *fiski* by the presence of a zone of small scales on the anterior aspect of the front foot immediately above the claws, instead of the large scales which he says continue to the base of the claws in *fiski*. We have been unable to verify whether this key character holds.

In all probability Boulenger (1886b) was induced to describe *fiski* by his overlooking Smith's (1839) mention of the presence of a conical tubercle on the hinder side of the thigh in *verroxii*, and also by the uncertainty as to the latter's type locality (which is possibly much nearer to that of *fiski* than has hitherto been supposed). Boulenger never saw a specimen of *verroxii* and, as recently as April 6, 1954, Mr. J. C. Battersby assures us that there are no representatives of the species in the British Museum, i.e. all their material is referred to *fiski*. When at the British Museum in 1953, one of us (E. E. W.) studied the types of

fiski, seimundi and *smithi*, and shortly afterwards at Senckenberg the type of *boettgeri=oscarboettgeri*. Paratypes of *schonlandi* (M.C.Z. 42222-4) have been available to us also.

Description. Beak weakly or strongly hooked, tricuspid, edge of jaws finely dentate; prefrontal and frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few extremely large (in some instances a single shield is exceptionally enlarged as in *oculifer*), unequal, juxtaposed, subimbricate scutes, forming 2-4 longitudinal and 5-9 transverse series

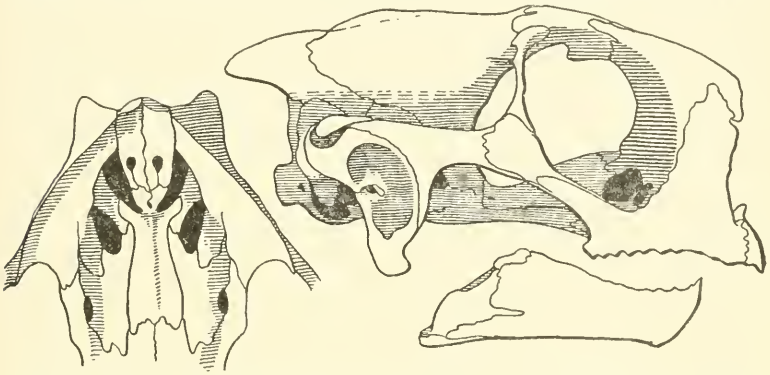


Fig. 32. Skull of *Psammobates t. verroxii* juv. (M.C.Z. 21330). Condylobasal length 15 mm. The youth of the specimen is reflected in the very open sutures.

(S. McDowell del.)

from elbow to outer claw; claws 5; hinder side of thigh with one or more enlarged, conical tubercles;[1] heel with a large spurlike tubercle; claws 4, rarely 5.

Carapace more or less convex, sides rounded, descending abruptly, very shallowly notched in nuchal region, anterior and posterior margins more or less expanded, sometimes reverted, and not or but slightly serrated; dorsal shields concentrically striated; nuchal usually present, typically broader than long or slightly longer than broad, rarely divided,[2] frequently minute, rarely absent; vertebrals 5, rarely 4[3] or 6,[4] more or less swollen,

[1] In stating "without" Boulenger (1889a) misread Smith's description.
[2] In type of *depressa* FitzSimons.
[3] *Fide* Power (1933a).
[4] In type of *scimundi* as well as other specimens.

much broader than long, as broad as, broader than, or narrower than, the costals; costals 4, rarely 5,[1] usually not forming an angle with the lateral marginals; marginals 11 or 12; supracaudal undivided, incurved in ♂ ♂, inclined to spread out like marginals in ♀ ♀; tail in ♂ ♂ usually devoid of lateral tubercles, if present, small, in ♀ ♀ large lateral tubercles present, both sexes without a terminal clawlike tubercle.

Front lobe of plastron usually anteriorly truncate, occasionally somewhat produced,[2] openly notched; gulars paired, rarely subdivided;[3] pectorals more or less narrow where they meet, their anterior border sloping more or less steeply towards the axillary notch; axillaries 2 or 3, rarely 1, one large and the others, if present, small; inguinal moderate to large, sometimes with 1 or 2 supplementary shields, meeting femoral; hind lobe more or less deeply notched posteriorly.

Plastral formula: Abd>h>an>or<g>or=f>or<p. Anal typically longer than g or f; p usually shortest.

Color. Carapace light to brownish yellow, the yellow on each dorsal shield usually subequal in width to the 5 or 6 black rays of which the anterior and posterior pairs on vertebrals and costals meet their fellows to form three series of ocelli. At times the black rays may coalesce so that black predominates; marginals with 1 to 3 black rays. Plastron yellow, sometimes uniform, though normally its median portion is variegated with dark brown.

The plastral pattern in the type of *smithi* approaches that of *tentorius trimeni*. Separation of *smithi* and *boettgeri* from *verroxii* on the grounds that their light rays are yellow (instead of red and yellow as in *verroxii*) appears unjustifiable.

The type ♂ of *seimundi* had a yellowish horn-colored carapace from the centre of whose shields radiated short or interrupted, blackish-brown striae; the plastron was similarly colored with mere traces of the dark radiating striae. The head showed a few dark brown specks, otherwise the soft parts were yellow.

The type ♂ of *H. bergeri*, based on a native *buchu*-box shell, was described as having a carapace that was uniform bright reddish horn-brown except for the bright yellowish areolae.

[1] In a Cape tortoise, *fide* Siebenrock.

[2] In type of *seimundi*.

[3] *Fide* Power (1932b), whom see for a very detailed study of *verroxii*.

Plastron horn-yellow, its central portion washed with bright reddish brown and a few obscure brownish rays. However, the specimen from Upington, Gordonia, reported on by Siebenrock (1910), had a chestnut brown carapace, each shield edged with darker of varying intensity while the center of the areolae tended to be lighter. Plastron light green, its central portion brownish. Head and limbs gray brown; outer scales on the forelimbs beautifully tinted with light brown. A specimen from Barby (now in the British Museum), which we have seen, corresponds very closely to Siebenrock's description. The Hereroland *bergeri* mentioned by Werner (1910a) had: Carapace red brown, uniform. Plastron yellow. Femoral and anal region brown. Sternfeld (1911b) concluded that *bergeri* was nothing more than a color variant.

In the type ♂ of *depressa* the head is described as being dirty yellow with more or less symmetrical blackish margins, viz. a bar down the front of the snout, a spot on top of the snout, a large spot above each orbit, and a crossbar on the back of the head. For full description of the shell cf. FitzSimons (1938).

Size. The type ♂ of *verroxii* was only 93.1 mm.; the type ♂ of *depressa,* 109 mm., its width 82 mm., breadth 50 mm. Carapace length of largest ♂ (ex Niekerk's Hope), 117.5 mm.; that of the largest ♀ (ex Ukamas), 141 mm., width 102.5 mm., height 74 mm. (*fide* Hewitt:1934)

Power (1933a) supplies data to show that ♂ ♂ average smaller than ♀ ♀, which bears out the importance of limiting comparisons to individuals of the same sex. Siebenrock's (1910) suggestion, accepted by Power, that there is a size and habitus difference justifying the separation of *fiski* from *verroxii*, is not supported by the available data.

Breeding. Females collected in April and May held only unripe ova. In October there was a single enlarged ovum besides several smaller ones. In December the oviduct contained a single shelled egg, besides several smaller ova. From this Power (1932b) deduces that a single egg is laid each year, and that this does not hatch until the following spring.

Diet. In the intestines of tortoises from Niekerkshoop one of the Crassulaceae was most frequently present, besides fragments of quartz. Each of these formed the core of a pellet of

vegetable matter averaging about 12 x 18 mm. in size; such pellets were surprisingly numerous, no fewer than twenty-six being present in one tortoise (Power:1932b).

Feeds on the *Mesembryanthemum* bushes beneath which these tortoises shelter at Aus (FitzSimons, writing of *boettgeri*: 1935a).

Parasites. Every tortoise in the large series collected at Niekerkshoop by Power (1932b) was infested with spirillum ticks (*Ornithodoros moubata*), especially about the neck where, in some instances, they formed solid masses.

Thread worms of several species referable to the Oxyuridae, were invariably present in the large intestine at its junction with the small intestine.

Habitat. South of the Orange River *verroxii* was found on the flats by Power (1932b), but at Niekerkshoop north of the river *verroxii* was restricted to koppies and *oculifer* to the sandy plains.

Localities. Orange Free State: "near the sources of the Orange River" (for type of *verroxii*, which Power would place here). *Cape Province:* Abiam, Gordonia district; Albany district; Alweynsfontein; Amandelbom Mission, Zak River; Beaufort West; Brandvlei; Britstown; Britstown to Victoria West; Bros Pan; Bros Pan to Wyksvlei; Burghersdorp; Colesberg; Concordia; De Aar; Deelfontein; Gamoep; Gamoep to Alweynsfontein (Alwijnsfontein); Graaf Reinet; *Hanover (U.S.N.M.); Hopetown; Houmoed; Keimoes; Leliefontein (Liliefontein); Little Namaqualand; Marydale; Middleburg; Molopo River — lower; Naauwpoort; Niekerkshoop (Niekerk's Hope); O'okiep; Orange River Station; Philipstown to Petrusville; Plaatjiesfontein near Dwaal; Prieska; Richmond; Richmond to Victoria West; Sea-cow River; Somerset East district; South Gordonia; Springbok (Springbokfontein); Springfield — near; *Steinkopf; Ukamas; Upington; Van Wyksvlei; *Victoria West. *Southwest Africa:* Augustfelde and Plateau Farms, Aus district; Aus (Oas); *Barby, Tiraz Mountains (Brit. Mus.); Bethany; Gibeon; Great Namaqualand; Jakalswater; Karas Mtns.; Keetmanshoop; Keibib; Keimoes; Klein Karas Mtns.; Klein Windhoek; Kubub; Kuibis;; Narudas Sud; Rehoboth.

Range. Possibly southern Orange Free State (for type only),

northern Cape Province (from Burghersdorp east to Williston and northwest to O'okiep, northwards through) Southwest Africa (Great Namaqualand to Rehoboth on the Tropic of Capricorn and the solitary 1895 record of Oudemans for Jakalswater near Swakopmund).

We consider erroneous the records of *verroxii* and *smithi* from the Blaauw Mountains, west of the Zoutpansberg range in the northern Transvaal. Siebenrock (1910) himself thought the data was questionable, being so remote from the general range of the species.

PSAMMOBATES TENTORIUS TRIMENI (Boulenger)

1886b. *Testudo trimeni* Boulenger, Proc. Zool. Soc. London, p. 541, col. pl. lvii: Mouth of Orange River, Little Namaqualand, Cape Province.
1889. Boettger, 283.
1889a. Boulenger, 163.
1893a. Boettger, 10.
1898. Sclater, W. L., 97.
1904c. Siebenrock, 320.
1907a. Duerden, 10.
1907c. Duerden, 199.
1909a. Siebenrock, 526.
1910. Siebenrock, 715.
1910a. Werner, 303.
1911d. Sternfeld, 50, fig. 63.
1914a. Hewitt, 247.
1929. Flower, 30.
1934a. Mertens and Müller *in* Rust, 9.
1955a. Mertens (part), 36, pl. iv, fig. 13.
1907b. *Testudo tentoria* var. *fiskii* Duerden (part, not of Boulenger), pl. viii, fig. 11.
1933b. *Chersinella tentoria hexensis* Hewitt, Ann. Natal Mus., 7, p. 286, pl. xv, figs. 39-40: Hex River, Worcester District, Cape Province.
1933b. *Chersinella trimeni* Hewitt, 287, pl. xv, figs. 41-45.
1934. Hewitt, 337.
1935a. FitzSimons, 521.
1937a. *Psammobates trimeni* Hewitt, 791, fig. 1.
1938. FitzSimons, 155.

Common name. Western Tent-Tortoise.

Illustrations. That of Boulenger (1886b) is the best, but those of Duerden (1907b) showing plastral view of alleged "*fiskii*" (error), and Hewitt (1933b) illustrating variations, give a good idea of this race.

Types. The three cotypes in the British Museum have been studied by one of us (E. E. W.); a fourth is preserved in the South African Museum (*fide* Sclater:1898).

Description. Beak scarcely or distinctly hooked, bicuspid, edge of jaws not or but weakly dentate; prefrontal divided longitudinally or broken up; frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few extremely large, unequal, juxtaposed scutes, of which one is often strikingly larger than the others, forming 1-3 longitudinal and 4-6 transverse series from elbow to outer claw; claws 5; hinder side of thigh with or without a never-very-large, flat or subconical tubercle; heel without definite spurlike tubercle; claws 4; tail in ♂ ♂ devoid of lateral tubercles, which are present in ♀ ♀, both sexes without a terminal clawlike tubercle.

Carapace convex, sides rounded, shallowly to deeply notched in nuchal region, anterior and posterior margins not expanded, slightly reverted, and moderately serrated;[1] dorsal shields concentrically striated; nuchal moderate, small, minute, or rarely absent; vertebrals 5, more or less convex, typically conical, broader than long, as broad as, or broader than, or narrower than, the costals; costals 4, forming an angle with the lateral marginals, which are convex and consequently separated from the costals by a well-defined longitudinal groove; marginals 11 or 12; supracaudal undivided, incurved in ♂ ♂, downwardly directed in ♀ ♀.

Front lobe of plastron anteriorly truncate, openly notched; gulars paired; pectorals moderately broad, their anterior border sloping slightly towards the axillary notch; axillaries 1-2, moderate; inguinal moderate to large, sometimes with 1-2 supplementary shields,[2] meeting femoral; hind lobe deeply notched posteriorly.

Plastral formula: Abd>h>or=(p, an)>or=g.

Color. Carapace yellow or orange (occasionally salmon red in life, *fide* Hewitt), the light rays on each dorsal shield narrower than the 4-8 black rays so that black predominates. Plastron yel-

[1] In which respect we disagree with Duerden (1907c) who considered this species non-serrate.

[2] *Fide* Duerden (1907c); we have also seen them with one such supplementary shield.

low, its central portion occupied by a broad black figure either indented with lighter or variegated with light rays.

Snout yellow with a median black line and similar lateral ones, side of head with a longitudinal suborbital bar terminating in a roundish postorbital spot; crown of head black. Cf. Hewitt (1933b:290) for color in life of soft parts of Bitterfontein specimens, and FitzSimons (1935a) for the juvenile coloring of a Lekkersing tortoise that he assigns to *trimeni*.

Size. Carapace length of largest ♂ (M.C.Z. 33451), 97 mm., breadth 75 mm., height 52 mm. Carapace length of largest ♀ (T.M. 16002), 121 mm., breadth 95 mm., height 67 mm.

Sexual dimorphism. According to Hewitt (1933b:290), supported by our ♂ and ♀, ♂ ♂ lack the patch of enlarged scales on side of tail which are present in the ♀ ♀, whose tails — as usual — are shorter.

Hewitt also claims that the foreheads of ♂ ♂ are more protuberant, and that this is correlated with a broad, downwardly projecting beak that bears a well-developed median, and two lateral, ridges. He asserts that the beak, when pronounced in ♀ ♀, lacks the sharp ridges. Hewitt also thinks that the lobes of the plastron converge less strongly in ♂ ♂ and that this results in the gulars and apical distance between the anals being broader than in the ♀ ♀.

Breeding. An egg, measuring 24.0 x 34.5 mm., was obtained from a ♀ taken near Bitterfontein (Hewitt:1933b).

Habits. During normal summer weather, according to B. Peers (in Hewitt:1933b) Trimen's Tent-Tortoises emerge to feed in the early morning and late afternoon. Upon the approach of unfavorable weather they seek shelter beneath some low-lying bush or euphorbia where they soon bury themselves by excavating the sand, first with the left forefoot, then with the right. Once completely covered they remain dormant until the arrival of cool weather or rain. Following a heavy downpour great numbers of tortoises emerge simultaneously so that many may be captured in a short time. While the rain is falling, according to Peers, whose description, however, is none too clear, the reptile raises its hind legs high so that the grooved shell, aided by the forelimbs, conducts the water to the corners of its mouth where it is eagerly taken in.

Habitat. The sandveld (Peers).

Localities. Cape Province — Little Namaqualand: Anenous — near; Calvinia — near;[1] *Bitterfontein — near; *Lekkersing;[1] Nieuwerust;[1] Orange River Mouth[1] (type locality); *Steinkopf; Van Rhyn's Pass — near, between Van Rhynsdorp and Nieuwhoudtville. *Southwest Africa* — Great Namaqualand: Augustfelde and Plateau Farms, Aus district; Keetmanshoop; 70 km. south of Walfish Bay (W. Triebner coll.).

Range. Extreme western Cape Province (i.e. Little Namaqualand) from Lambert's Bay (extending eastwards into Bushmanland according to Peers,[2] though we are unaware of any records from that area) north to the Orange River, and even occurring north of the river in Great Namaqualand (see discussion p. 310 above).

The record of *trimeni* from Kamelslip on the Nosop River, Bechuanaland, was based on a *buchu*-pouch carapace, i.e. a receptacle for the sweet-scented powder the natives obtain from the *buchu* plant. As this is the only occurrence of *trimeni* in Bechuanaland we reject the record, assuming the shell to have been carried to Kamelslip by its peripatetic owner.

The Clanwilliam and Stellenbosch records mentioned by Siebenrock (1910) as taken from Duerden (1907a), were stated by the latter to be only the home addresses of the donors.

Psammobates tentorius tentorius (Bell)

1828a. *Testudo tentoria* Bell, Zool. Jour., **3**, p. 420: Africa?
1836. Bell, text and col. pl. —.
1872b. Gray, 3, *in* Sowerby and Lear, pl. xiv.
1886b. Boulenger, 541.
1889. Boettger, 284.
1889a. Boulenger, 164.
1892. Müller, F., 214.
1893. Trimen, 79.
1897. Siebenrock, 247, pl. i, fig. 4.
1898. Sclater, W. L., 97.
1904c. Siebenrock, 321.
1907a. Duerden, 10 (a few localities are referable to *t. verroxii*).
1907b. Duerden, 74, pl. vii, fig. 8; pl. viii, fig. 10.
1907c. Duerden, 197.

[1] In Transvaal Museum, but seen by us.
[2] Cited by Hewitt (1933b).

1909a. Siebenrock, 527 (some of Duerden's *t. verroxii* localities accepted).
1914a. Hewitt, 247.
1929. Flower, 31.
1934a. Mertens and Müller *in* Rust, 9.
1937a. Flower, 9.
1939a. Müller, L., 129.
1954. Noël-Hume, 76.
1835. *Testudo geometrica* Temminck and Schlegel (part: not of Bell), 73.
1855. *Testudo geometrica* var. *nigriventris* Gray, Cat. Shield Rept., Brit. Mus., p. 8: South Africa.
1870b. *Peltastes tentorius* Gray, 9.
1870c. Gray, 656.
1873b. Gray, 9.
1898. *Testudo verreauxii* Sclater (not of Smith), 96 (Beaufort West).
1933b. *Chersinella tentoria* Hewitt, 265, pl. xiv, figs. 8-9.
1933b. *Chersinella tentoria albanica* Hewitt, Ann. Natal Mus., **7**, p. 266, pl. xiv, figs. 10-15: Mayfair, Albany District, Cape Province.
1933b. *Chersinella tentoria tentorioides* Hewitt, Ann. Natal Mus., **7**, p. 268, pl. xiv, fig. 16: Bowden Hall, Middlebury District, Cape Province.
1933b. *Chersinella tentoria piscatella* Hewitt, Ann. Natal Mus., **7**, p. 269, pl. xiv, figs. 17-18: Little Fish River, Somerset East District, Cape Province.
1933b. *Chersinella tentoria subsulcata* Hewitt, Ann. Natal Mus., **7**, p. 270: Brighton Farm, near Steytlerville, Cape Province.
1934. Hewitt, 336.
1933b. *Chersinella tentoria karuica* Hewitt, Ann. Natal Mus., **7**, p. 272, pl. xiv, figs. 19-24; pl. xv, figs. 25-28: Drogekloof Farm, near Klaarstroom, Prince Albert District, Cape Province.
1934. Hewitt, 336.
1933b. *Chersinella tentoria duerdeni* Hewitt, Ann. Natal Mus., **7**, p. 279, pl. xv, figs. 29-31: Graaf Reinet, Cape Province.
1933b. *Chersinella tentoria lativittata* Hewitt, Ann. Natal Mus., **7**, p. 281, pl. xv, figs. 32-34: Willowmore, Cape Province.
1933b. *Chersinella tentoria karuella* Hewitt, Ann. Natal Mus., **7**, p. 283, pl. xv, figs. 35-38: Uniondale, Cape Province.
1937a. *Psammobates tentoria* Hewitt, pl. x, fig. 5 (skull).
1937e. *Psammobates tentoria albanica* Hewitt, 7, pl. iii, figs. 1-2; pl. xxvii, fig. 9.
1937e. *Psammobates tentoria tentorioides* Hewitt, 8; also as "tent tortoise" skeletal shell, pl. xxviii, fig. 1.
1937e. *Psammobates tentoria piscatella* Hewitt, 8, pl. iii, fig. 3; pl. ivA, figs. 2-3.

1937e. *Psammobates tentoria duerdeni* Hewitt, pl. ii, fig. 3.
1946a. *Psammobates tentoria karruica* (*sic*) FitzSimons, 353.
1950. *Geometric Tortoise* Rose, fig. 206.

Further citations of "*tentoria*," also *tentoria hexensis*, will be found under *t. verroxii* and *t. trimeni*.

Common names. Southern Tent-Tortoise (preferred); South African Starred Tortoise (Noël-Hume:1954); *knoppiesdop* or *knoppiesskilpad* (Afrikaans, *fide* Hewitt:1937e).

Illustrations. Bell's (1836) fine picture of the type will not be available to most workers, who will be grateful to Hewitt (1933b and 1934) for his photographic reproductions of most of the outstanding variants.

Types. The type of *Testudo tentoria* Bell in the Oxford Museum has been examined by E. E. W.

Description. Beak weakly or strongly hooked, bi- or tricuspid; edge of jaws more or less serrate; prefrontal and frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few, extremely large, unequal, juxtaposed scutes, forming 2-4 longitudinal and 4-9 transverse series from elbow to outer claw; claws 5; hinder side of thigh with or without 1 or more, large, subconical tubercles; heel without definite spurlike tubercle; claws 4; tail in both sexes devoid of lateral tubercles and without a terminal clawlike tubercle.

Carapace convex, sides rounded, broadly notched in nuchal region, anterior margins slightly expanded, posterior sometimes reverted and slightly serrated; dorsal shields concentrically striated; nuchal occasionally well developed, usually small, minute, or even absent; vertebrals 5, rarely 6 or 7,[1] usually strongly conical[2] and, except for the first, usually broader than long, narrower than the costals; costals 4, occasionally 5, sometimes forming an angle with the lateral marginals; marginals 11-13; supracaudal undivided, incurved in ♂ ♂, downwardly directed in ♀ ♀.

Front lobe of plastron anteriorly truncate, openly notched; gulars paired; pectorals very variable, narrow or relatively broad, their anterior border curving or sloping towards the

[1] *Fide* Hewitt (1933b:271, 275, 277); 7 in U.S.N.M. 16225, seen by E.E.W.

[2] The degree of convexity is highly variable even in tortoises from the same locality, says Duerden (1907c: 189).

axillary notch; axillaries 2 or more, variable in size; inguinal moderate to large, sometimes with 1 or 2 supplementary shields, meeting femoral; hind lobe deeply notched posteriorly.

Plastral formula: Abd>h>or<g>or<an>or<f>p. Pectoral the shortest scute.

Color. Carapace yellow or orange, the light rays on each dorsal shield usually narrower than, though sometimes subequal to or broader than, the 8-14 black rays (8-12 on vertebrals, 12-14 on costals, 3-4 on marginals) so that black frequently predom-

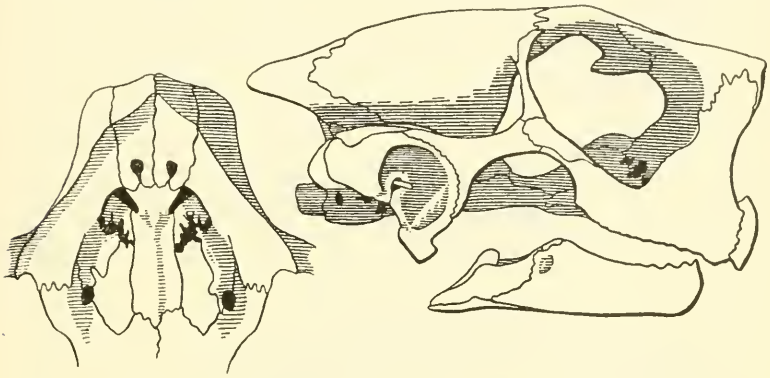


Fig. 33. Skull of *Psammobates t. tentorius* (M.C.Z. 3465). Condylobasal length 24 mm.

(S. McDowell del.)

inates. Plastron yellow, sometimes faintly tinged with orange, visible only on the periphery as the central portion is occupied by a broad brown figure.

The tail and adjacent soft skin are red to orange red (*fide* Hewitt:1933b).

Size. Carapace length of the type of *tentorius*, 108 mm. Carapace length of largest ♂ (ex Matjesfontein), 100 mm., breadth 74 mm., height 74 mm. (FitzSimons:1946a). Carapace length of largest ♀ (a paratype of *t. karuella*), 138 mm., breadth 107 mm., height 74 mm. (Hewitt:1933b).

Breeding. In September, 2 or 3 eggs are laid. Two oval eggs of "*albanica*" measured 21.3 x 27 mm. and 23.5 x 31 mm. respectively. Two tortoises that hatched out in May measured

25.4 mm. (given as 1 inch) in length (E. du Toit etc. in Hewitt: 1933b and 1937e).

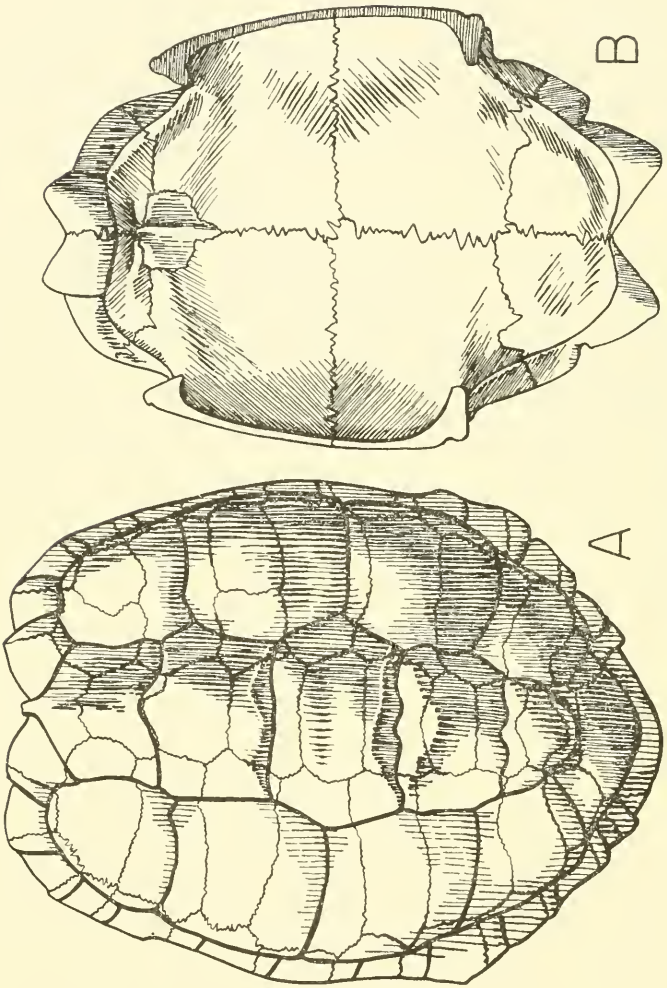


Fig. 34. *Psammobates t. tentorius* (B.M.). *A*, Dorsal view of carapace showing numerous abnormalities; *B*, Internal view of plastron.
(P. Washer del.)

Longevity. Seven years, 5 months, and 6 days for a specimen received at the London Zoo in 1920 (Flower:1937a).

Diet. In a wild state the diet includes *Eragrostis bergiana* (*fide* E. du Toit) lettuce and lucerne in captivity (Hewitt: 1937e).

Enemies. In certain areas ostriches, by devouring the young, have almost exterminated this form (Hewitt:1937e).

Habits. In June not a single tortoise was seen at Drogekloof, though the veld was traversed in every direction daily by Miss I. Z. Oosthuizen; in September — though there had been no rain and the veld was even drier — tortoises were encountered almost every day (Hewitt:1933b).

Tent-Tortoises in captivity develop regular habits, each reptile returning to its favorite corner of the pen after feeding or sunning. Rather more sluggish and timid than other species, the forelimbs, when withdrawn, completely conceal both the head and all surrounding skin (Hewitt:1937e).

Habitat. In the Albany district *tentorius* is found among low bushes in the karroid vegetation on either side of the Great Fish River (Hewitt:1937e).

Localities. Cape Province (but note remarks under Range): Abraham's Kraal, Prince Albert district; *Adendorp; *Beaufort West; Bowdon Hall, Middleburg district; Brandeston Farm, Albany district; Brighton Farm, Steytlerville; Calitzdorp (Calitsdorp); Carlisle Bridge; Dikkop Flats between Grahamstown and Port Elizabeth; Drogelkloof Farm near Klaarstroom; *Fish River near Grahamstown; Graaff Reinet; *Grahamstown; Kliplaat; Koup; Letjesbosch, between Beaufort West and Frazerburg Road; Little Fish River; Matjesfontein; Mayfair, Albany district; Middleton, Carlisle district; Muiskraal; Nelspoort; Oudtshoorn; Prince Albert; Steytlerville; Uniondale; *Upper Karroo; *Warmbad Farm, Uniondale (seen at U.S.N.M.); Welbedacht Farm, Olifants River, Oudtshoorn district; Westondale, Pearston district; Willowmore; Zwartruggens (Swart Ruggens), Aberdeen district.

Range. Southeast Cape Province, mostly south of the 32nd parallel. Typically concentrated in the region from Grahamstown to Uniondale. Apparently intergrading with *Psammobates tentorius verroxii* at Adendorp; Graff Reinet; Middleburgh dis-

trict (which is north of the 32nd parallel); Nelspoort and Beaufort West. At Matjesfontein and vicinity, intergrading with both *P. t. verroxii* and *P. t. trimeni* may be expected. Erroneously recorded from Mauritius by Gray (1873b).

Genus CHERSINA Gray

1831c. *Chersina* Gray (not of Humphreys: 1797),[1] Syn. Rept., pp. 7, 14, Type: *Testudo angulata* Schweigger (by monotypy).

1929. *Goniochersus* Lindholm, Zool. Anz., **81**, p. 285. Type: *Testudo angulata* Schweigger (by original designation).

1931. *Neotestudo* Hewitt, Ann. Natal Mus., **6**, p. 504. Type: *Testudo angulata* Schweigger (by original designation).

Definition. Skull with triturating surface of maxilla without ridging but a weak ridge on the horny sheath; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina moderately large, not concealed; prootic well exposed dorsally; quadrate enclosing stapes in adults; surangular subequal in height to prearticular; neck with second, third or fourth centrum biconvex.

Carapace never hinged; normally the anterior neurals hexagonal; outer side of third costal scute about as long as, or longer than, that of the fourth; submarginal scute absent; suprapygal 1.

Plastron not hinged; gular region greatly thickened and produced; gular shield *single*, much longer than broad.

Distinguishing marks. The only continental African tortoise with a single gular scute.

Range. Union of South Africa (Cape Province only), possibly extending into Southwest Africa.

Fossil record. None.

Remarks. We have separated the peculiar species *angulatus* from the genus *Testudo* on osteological grounds. An external character, the single gular, indeed suffices to set it apart from all the tortoises of continental Africa, but this condition is paralleled by the tortoises of Mauritius and Rodriguez and by the Malagasy species *yniphora*, all of which we refer to the genus *Geochelone*. From the *Geochelone* species with single gulars, *Chersina* differs in the very extensive thickening of the gular region, in which as in some other features it resembles *Kinixys*.

[1] See footnote 3 on page 218.

Not all of its features are resemblances to *Kinixys*, however, and its true affinities are doubtful.

To illustrate the problem and our method of meeting it we tabulate (Table 6) the characters of *Chersina* and cite for each of them the genera presenting the closest similarity.

TABLE 6

Chersina	Genera showing greatest resemblance	Comment
Maxilla with a very feeble ridge or none	No ridge in *Kinixys, Homopus, Pyxis, Psammobates;* reduced or absent in *Testudo*	An advanced character in which *C.* is intermediate
Quadrate closed behind stapes in adults	*Kinixys, Homopus, Psammobates, Testudo s. str., Malacochersus,* most *Geochelone,* and *Gopherus* and †*Stylemys*	An advanced character achieved in parallel by many genera
Anterior palatine foramina moderate to large	*Testudo*	An advanced character in which *C.* is somewhat intermediate
Anterior marginals elongate	*Kinixys*	A specialized character shared only with *K.*
Neurals variable approaching the octagonal and quadrilateral pattern	*Pyxis, Testudo, Geochelone, Gopherus*	An advanced character which *C.* appears to be approaching independently
Suprapygal single	*Kinixys, Pyxis, Acinixys, Psammobates, Testudo, Malacochersus*	A primitive character shared with emydines
Gular process greatly thickened and extended anteroposteriorly	*Kinixys*	A specialized character shared only with *K.*

From this tabulation it will be seen that except in neural pattern (*Kinixys* is obstinately hexagonal) and in the single gular, *Chersina* is either close to *Kinixys* or more primitive than that genus. If it were to be synonymized with any genus it would seem more reasonable to equate it with *Kinixys* than with *Testudo* or *Geochelone*. But the differences from *Kinixys* seem to us to imply a long separate history, and we are not certain that the relationship to *Kinixys* is as great as emphasis upon two specialized characters would suggest. We prefer therefore to regard this form as a full genus belonging to the series of Ethiopian endemics.

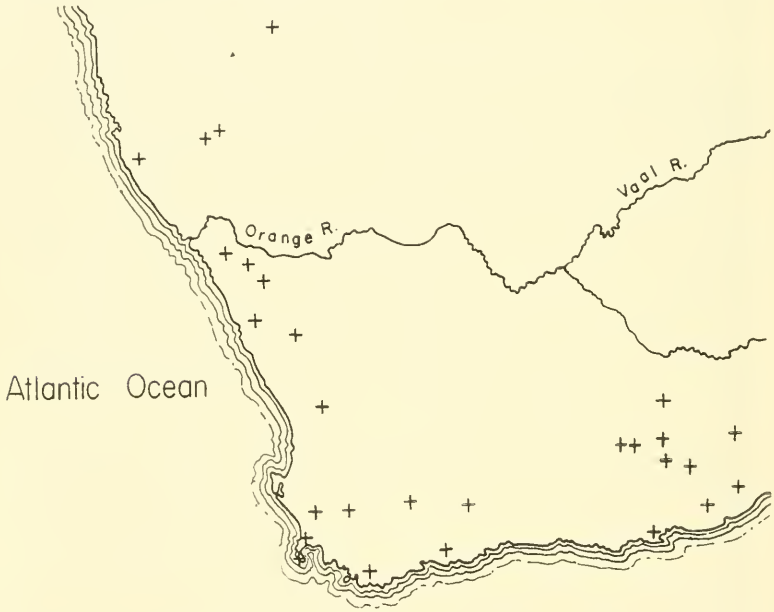


Fig. 35. Distribution of *Chersina angulata* in South Africa.
(P. Washer del.)

The distribution of this tortoise is wholly included within the range of *Psammobates*, possibly within that of *Homopus*.

There appears to be no clearly demarcated geographical variation within *angulata;* as to red on the plastron, see paragraph on *Color* below (p. 348).

Chersina angulata (Schweigger)

1795. *Testudo pusilla* Thunberg, (not Linnaeus, 1758), 3.
1812. *Testudo angulata* Schweigger, Königsberger Arch. Naturwiss. Math., 1, pp. 321, 360, 443: No locality.
1814. Schweigger, 52 (reprint of 1812).
1835. Duméril and Bibron, 130 (not 150).
1835. Temminck and Schlegel (? part *erosa*), 72.
1836. Bell, text and col. pl. —.
1845b. Rüppell, 297.
1857. Jan, 35.
1872b. Gray, 5, *in* Sowerby and Lear, pl. xix.
1889. Boettger, 286.
1889a. Boulenger, 178.
1889. Vaillant, 166, pl. xv, figs. A-B.
1890. Strauch, 57.
1892. Müller, F., 214.
1893a. Boettger, 12.
1898. Jeude, 5.
1898. Johnston, 361.
1898. Sclater, W. L., 97.
1901. Lampe, 194.
1907a. Duerden, 9-10 (only donor's addresses).
1907b. Duerden, 73, pl. vi, fig. 4.
1909a. Siebenrock, 543.
1910a. Werner, 305.
1911d. Sternfeld, 50.
1912b. Werner, 434.
1915. Werner, 331.
1925b. Flower, 932.
1928. Cott, 952.
1929. Flower, 30.
1929. Rose, 188, 225, 231, fig. 125.
1935a. FitzSimons, 519.
1937a. Flower, 9.
1937. Ruckes, 103, pl. x, fig. 4.
1950. Williams, 551.
1812. *Testudo tabulata Africana* Schweigger (not of Hermann), Königsberger Arch. Naturwiss. Math., p. 322: No locality.
1814. Schweigger, 54 (reprint of 1812).
1820. *Chersine pusilla* Merrem (not of Linnaeus: 1758), 38.
1946a. FitzSimons, 354.

1828. *Testudo Bellii* Gray, Spicilegia Zoologica, p. 2, pl. iv, figs. 3-3a: Cape of Good Hope.
1831c. *Chersina angulata* Gray, 15, pls. i-ii.
1831b. Gray, 5.
1844. Gray, 11.
1849. Smith, A., App., 1.
1855. Gray, 12.
1860. Fitzinger, 411.
1862a. Strauch, 23.
1865. Strauch, 36.
1866. Gray (part), 306.
1867a. Steindachner, 4.
1870e. Gray (part), 13.
1873b. Gray, 14.
1873c. Gray, 726, pl. lx, fig. 6.
1873h. Gray, 496.
1885. Smets, 2 (locality erroneous).
1887b. Boettger, 137.
1887a. Müller, F., 296.
1931. *Neotestudo angulata* Hewitt, 504.
1934a. *Goniochersus angulatus* Mertens and Müller *in* Rust, 63.
1955a. Mertens, 34, pl. iii, fig. 14.
1937a. *Chersine angulata* Hewitt, 789, pl. x, fig. 7.
1937e. Hewitt, 6, pl. i, fig. 3; pl. iv, fig. 4; pl. xxvii, fig. 10.
1938. FitzSimons, 153.
1950. Rose, 325, 343, figs. 207-208.
1946. *Testudo* (*Chersine*) *angulata* Cairncross, 396.

Synonymy. Schweigger (1812) took the name *Testudo angulata* from a specimen labeled by Duméril in the Paris Museum; authorship was later claimed by Duméril and Bibron (1835: 130 and 138). *T. tabulata africana* Schweigger (not of Hermann) was also based on a Paris Museum tortoise. Strauch (1862a:67) has explained why *Testudo pusilla* Linnaeus (1758: 199) is not identical with *pusilla* Linnaeus (1766:353). The latter, being preoccupied, cannot be used, as was done by FitzSimons (1946a:354). FitzSimons (1938) suggested that *Chersina* Gray 1831, having been proposed by Humphreys for a gastropod in 1797, is not available, hence his use of *Chersine* Merrem (see however, footnote 3, p. 218).

Common names. Angulated Tortoise (Hewitt:1937e); Bowsprit Tortoise (Flower:1929); bont-skilpad; duine-skilpad;

ploegskaar-skilpad; rooi-skilpad; skaar-skilpad (Afrikaans, all Hewitt:1937e).

Illustrations. There are excellent figures in Gray (1831:pls. i-ii), and Bell (1836), the latter reproduced in Sowerby and Lear (1872:pl. xix).

Description. Beak weakly or strongly hooked, bi- or tricuspid, edge of jaws very weakly serrate; prefrontal divided longitudinally, sometimes separated from the frontal by a small scale; frontal large, or occasionally divided longitudinally,[1] flanked by 4-5 small scales; upper head shields small, irregular; forelimb, more especially anteroventrally, with several rows of moderately large, subequal, juxtaposed or slightly separated scutes forming 2-3 longitudinal and 7-9 transverse series from elbow

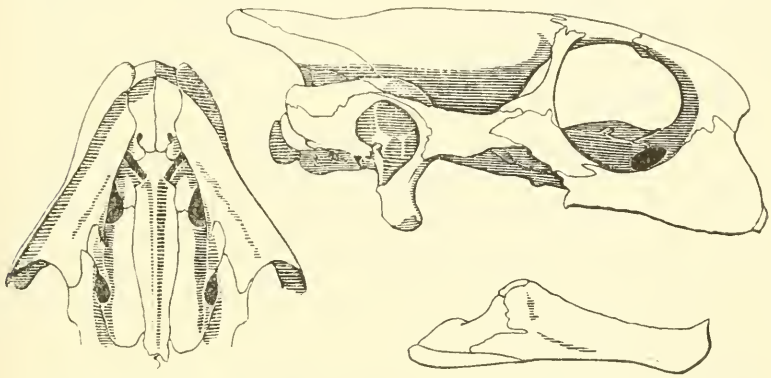


Fig. 36. Skull of *Chersina angulata* (B.M. 67-4-2-152). Condylobasal length 28 mm.

(S. McDowell del.)

(on the lower or inner side of which is an isolated large scute) to outer claw; on the upper or outer aspect of the wrist is a semi-bracelet of large scutes; claws 5; hinder side of thigh without large tubercles; heel with one or more enlarged flat scales; tail without terminal clawlike tubercle.

Carapace elongate, moderately convex, sides descending abruptly, deeply notched in nuchal region, anterior margins expanded but neither reverted nor serrated, posterior margins not or but moderately expanded, reverted, somewhat sinuate; dorsal

[1] Divided in a Steinkopf specimen, *fide* Werner (1910a).

shields concentrically striated except in aged specimens, neither swollen nor convex; nuchal narrow, elongate, always small, sometimes absent;[1] vertebrals 5, rarely 6 or 7,[2] flat, the first about as broad as long or longer than broad, the second, third and fourth much broader than long, the fifth broader than long or longer than broad, the third narrower than the third costals; costals 4, rarely 5,[3] usually not forming an angle with the marginals; marginals 11, rarely 10;[4] supracaudal undivided, more or less incurved in ♂ ♂, downwardly directed in ♀ ♀.

Front lobe of plastron always strongly produced, its end truncate or rounded; gular entire;[5] pectorals narrow where they meet, their anterior border sloping steeply towards the axillary notch in adults, less so in young; axillaries 1 or 2 (single in young, double in adults) moderate; inguinal large, meeting femoral; hind lobe deeply notched posteriorly in ♂ ♂, more shallowly in ♀ ♀.

Plastral formula, adults: Abd>g>h>or<an>f>or=p; juveniles: Abd>h>g>an>p>f.

Color. In both juvenile and adult the carapace is pale straw or pale horn to olive, the areola of each vertebral and costal shield usually darker and the periphery broadly margined with black, these borders occasionally interrupted by lighter rays; a broad-based, black, triangular blotch on the sutures between marginals; supracaudal with a median, down-pointing, black triangular mark. Sometimes, however, the pattern may be broken up, indistinct.

Plastron pale straw to yellow; from gular to anals extends a broad, black blotch, uniform, variegated with lighter, or broken up, its borders not sharply defined; lower aspect of lateral marginals yellow, but those posterior to the inguinal tend to display a black blotch at their anterior edge, and there may be a similar spot on one of the anterior marginals.

[1] Absent in a Richtersveld tortoise (M.C.Z. 42211).

[2] Six in a Great Namaqualand buchu pouch, *fide* Boettger (1889); 7 in a Steinkopf hatchling (M.C.Z. 42210).

[3] Five in a Great Namaqualand buchu pouch, *fide* Boettger (1889).

[4] Ten on right side of a Steinkopf hatchling (M.C.Z. 42210).

[5] Semidivided on the lower surface of an adult ♂ from Penrock, *fide* Hewitt (1931; see also Ilewitt:1937a:790). In Rose's figure (1950:343) the gular is called a "subgular", while the humerals are miscalled "gulars" and the pectorals "humerals."

In life the plastron is said to be reddish by Bell (1836) but the color disappears soon after death. However, Duerden

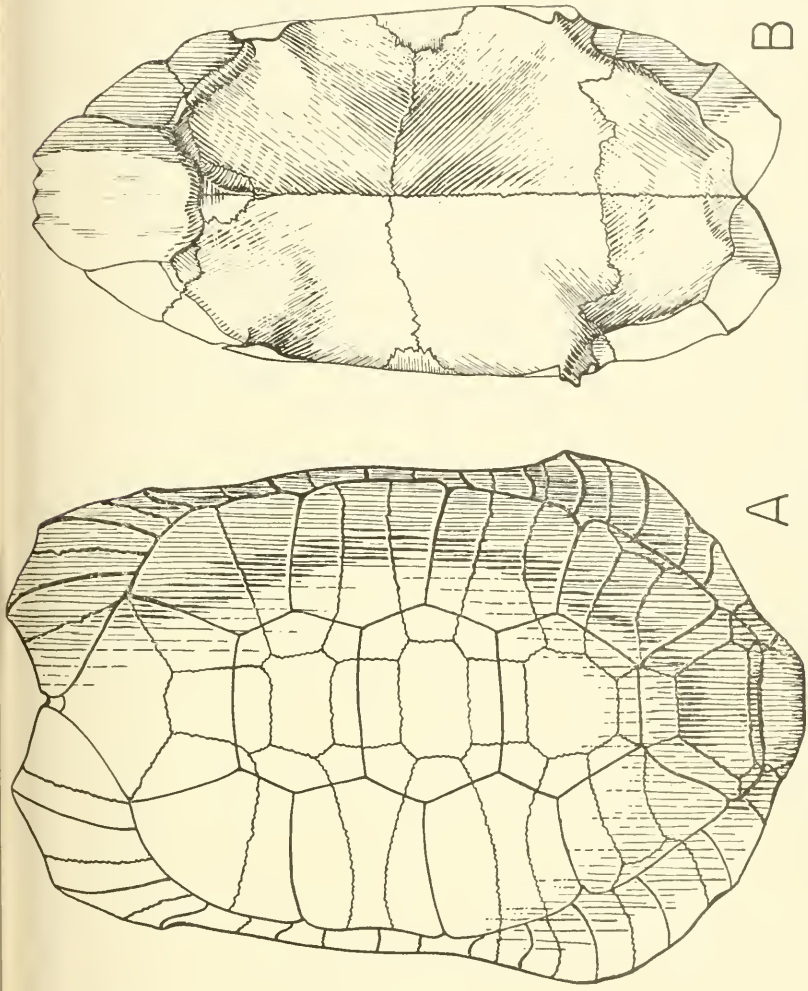


Fig. 37. *Chersina angulata* (M.C.Z. 52250) from South Africa. *A*, Dorsal view of carapace, (x ⅔); *B*, Internal view of plastron, (x ⅔). (P. Washer del.)

(1907b:74), seemingly suggesting that it is a local characteristic, remarks that *angulata* from the western part of Cape Province possess plastrons having a diffusely reddish ground color. FitzSimons (1935a) states that the sides of the plastron are suffused with reddish in adults, especially so in ♂♂ from Van Rhynsdorp, and later (1938) remarks on the bright rosy red plastrons of Kamieskroon and Klipfontein tortoises.

Snout at tip, and hinder part of head, black; prefrontal and frontal shields yellow (Hewitt:1937e). The coloring of the soft parts as given by Gray (1866:306, etc.) was based on the head and limbs of a *Geoemyda punctularia* associated with the shell of an *angulata* (*fide* Boulenger:1889a:178).

Size. Carapace length of largest ♂, 264 mm., breadth 59 mm. (Hewitt:1937e), length of another ♂ (M.C.Z. 3998), 183 mm., breadth 112 mm., height 80 mm. Carapace length of largest ♀ (T.M. 15996), 163 mm., breadth 104 mm., height 81 mm. (from Soebartsfontein, FitzSimons:1935a); length of a Port Elizabeth ♀ (M.C.Z. 9328) 153 mm., breadth 103 mm., height 68 mm.

Weight. The largest ♂ listed above weighed 5 lbs. (Hewitt: 1937e). See also Cairncross (1946:397) for tabulated increases among hatchlings.

Sexual dimorphism. The rather spadelike projection of the front lobe of the plastron is much more strongly produced in ♂♂ (whose plastron is also somewhat concave in its posterior third) than in ♀♀ (whose tails are noticeably shorter than those of the ♂♂). These sexual differences have been well illustrated in black and white by Vaillant (1889:pl. xv=our Plate 12).

Breeding. In August, at Cape Town, the ♀ digs a nest hole of from 3 to 4 inches in depth; only a single egg is laid (Rose: 1950). However, two eggs (M.C.Z. 21662) were laid on 18.viii. 1925 at the M.C.Z. by a Port Elizabeth tortoise (M.C.Z. 22475). Eggs, though usually oval, are sometimes spherical, rarely pointed at one end. In size they range from 35 x 37 mm. to 34 x 42 mm. (Hewitt:1937e:pl. xxvii, fig. 10).

While the incubation period at Cape Town may range from 12 to 14 months (Rose:1950), Cairncross mentions a 30-grain egg laid on 7.v.40 which, placed in an incubator on 3.viii.40, hatched on 3.xi.40, i.e. in 6 months; however, the hatchling was

malformed and died 14.x.41. For growth and weight records of other hatchlings, see Cairncross (1946:397). The hatchling's carapace is flat and strikingly different from the convex shell of the adult (Hewitt:1937e).

Rose managed to protect the egg from rats and other predators by disinterring it and then reburying it at the same depth of soil within a wire basket sunk in the ground and securely covered over by wire netting.

Longevity. Eleven years, nine months in Giza Zoo (Flower: 1925b; 1937a).

Diet. Eats gazanias (A. Rothmann); fond of young beans and regarded as a nuisance by gardeners (Hewitt:1937e); a captive specimen displayed a liking for meat (Rose:1950) but this author's somewhat contradictory statement that true tortoises are "normally strictly vegetarian" should have the second adjective omitted.

Enemies. Unquestionably man. Writing from Mrs. Müller's farm, apparently a day's trek northeast of Cape Town, on September 11, 1773, Thunberg (1795:3) says: "Among the bushes in the sands we frequently saw land-tortoises crawling, and the young ladies in the house had ordered the slaves to bring several of them home of various sizes for our repast. The *Testudo pusilla* was the most common species here, and it was this which was now laid upon the fire for our eating. I slipped into the kitchen on purpose to see the mode of dressing it, and found that the girls were cruel enough to lay the poor animal wide open on the live coals, where, sprawling with its head and feet, it was broiled alive, till at length it burst to pieces with the heat. The eggs, which were in great number, and consisted of yolk only, were the most luscious and desirable part of it."

The 21 young tortoises, with unbroken shells about two inches in diameter, recovered from the stomach of a ♂ Secretary Bird (*Sagittarius serpentarius*) killed on the Cape Flats by Levaillant (1824, Hist. Nat. Oiseaux d'Afrique, 1:70, pl. xxv), were probably referable to *angulata* suggests Rose (1950:344).

Temperament. Males spend much time in sparring with their rivals (Hewitt:1937e). One ♂, by biting the heads of other ♂ ♂ in the enclosure, induced them to withdraw into their shells, whereupon he would thrust his nose or *plastral projection* be-

neath their shells and so overturn them. Occasionally he would achieve the same result by butting them head on, then walk away leaving his opponents sprawling on their backs (Rose:1950). Females do not respond readily to a male's advances, in fact they usually endeavor to escape him by running away (Cairncross:1946).

Habitat. The drier coastal and central districts of Cape Province as far eastwards as the Keiskama (Hewitt:1937a). Still occurs on the Cape Flats, but is more often met with on the less-frequented uplands towards Cape Point (Rose:1950).

Localities. Cape Province:[1] Adelaide; *Cape of Good Hope; Cape Flats; Cape Point; Cradock; Dassen Island (introduced); Fish River Valley; Grahamstown; Graaff Reinet; Kamieskroon; Keiskama Valley; Kenkelbosch; Klipfontein; Malmesbury; Matjesfontein; Mortimer; Penrock near Grahamstown; *Port Elizabeth; Queenstown; *Richtersveld; Lekkersing; Rhynheath; Schoombie; Soebatsfontein; *Steinkopf; Stillbay; Van Rhynsdorp; Welbedacht; Worcester; Zoetendahl's Valley. *Southwest Africa:*[2] Bethany (based on buchu pouches collected by Schinz, etc. Boettger: 1887b); Karibib (Shell:Mertens:1955a); Kuibis (shell lacking anterior lobe of plastron, so possibly native preserved. Werner:1915); Orange River mouth (2 live ♀ ♀, coll. G. May); *Pomona (A.M.N.H., alcoholic); Rietmond near Gibeon (Lampe:1901).

Range. Cape Province west of 28° East longitude, possibly extending northwards into Southwest Africa.

Erroneously recorded from West Africa and Madagascar by Bell (1836); from Natal by Jan (1857); from Matabeleland and Zambezi region by Smets (1885); and the East Indies by Burmeister (not seen).

Genus HOMOPUS Duméril and Bibron

1835. *Homopus* Duméril and Bibron, Erpét. Gén., **2**, p. 145. Type: *Testudo areolata* Thunberg (designation by Fitzinger: 1843: 29).

1835. *Chersobius* Fitzinger, Ann. Wiener Mus., **1**, pp. 108, 112, 122. Type: *Testudo signata* Schoepff (by original designation).

[1] In an annual report Duerden (1907a) lists *angulata* from 14 donors, whose addresses he gives, but these we omit as there is no way of telling whether the specimens actually came from the places mentioned.

[2] The records from Southwest Africa should be investigated, a statement with which Mertens (1955a) concurs.

1931. *Pseudomopus* Hewitt, Ann. Natal Mus., **6**, pp. 496, 498. Type: *Testudo signata* Schoepff (by original designation).

Definition. Skull with triturating surfaces of maxilla and premaxilla without ridges; maxillary not entering roof of palate; anterior palatine foramina moderate to large, conspicuous; prootic narrowly exposed dorsally; quadrate enclosing stapes; surangular subequal in height to the prearticular; neck with third centrum biconvex.

Carapace never hinged; normally the anterior neurals hexagonal or quadrate; outer side of third costal scute longer than that of fourth; submarginal scute absent; suprapygals 2, the anterior larger, bifurcating posteriorly to embrace the smaller posterior element which is adjacent to, but not crossed by, the sulcus between the fifth vertebral and the supracaudal.

Plastron not hinged; gular region slightly thickened and produced; gular shields paired, usually broader than long.

Range. Union of South Africa (western Orange Free State and Cape Province), possibly extending into Southwest Africa.

Fossil record. None.

Homopus alone of the present day Ethiopian endemic tortoise genera has been alleged to have a fossil record. In 1889 Lydekker (Cat. Foss. Rept. Brit. Mus., part 3, p. 91 seq.) assigned †*Emys comptoni* Bell, of the London Clay Eocene of England, and †*Emys scutella* v. Meyer, from the Oeningen Upper Miocene of Switzerland, to *Homopus*. Bell, as Lydekker points out, when describing †*E. comptoni*, indicated resemblances to *H. areolatus* and *H. signatus* and was probably only deterred from referring the species to *Homopus* by the fact that the London Clay is a marine deposit.

Since Lydekker's time little attention has been paid to these fossils. Hewitt (1937a:792) justly remarked: "It is interesting to note that flattened shells of similar form and size to *Homopus* did occur so long ago in Europe, but the generic identity should be considered very doubtful, as the characters emphasized are quite insufficient."

Fortunately one of us (E.E.W.) has been able to examine material of both of these fossil species — the unique type of †*comptoni* in the British Museum and two specimens of †*scutella* in

the Teyler Museum, Haarlem, Holland. The Teyler Museum generously permitted the specimens of †*scutella* to be borrowed and further prepared. Only one side of each had been exposed; skillful preparation by Mr. Arnold Lewis of the Museum of Comparative Zoology has now revealed the other side in each specimen, despite the extreme rottenness of the bone in places.

Whereas superficial examination of this material had seemed to support, or at last did not refute, the assignment to *Homopus*, the more careful study now possible reveals that neither species can be referred to the South African genus. Instead, on totality of characters, both appear referable to *Testudo*.

The type specimen of *comptoni* is defective in various critical areas, and probably could not be placed with certainty were it not that †*scutella*, which it so much resembles, furnishes a guide to its assignment. The two species are considered to be *Testudo* rather than *Homopus* on the following characters:

1. The neural pattern is advanced in both species; already incipiently octagonal *cum* quadrilateral anteriorly in Eocene †*comptoni*, and definitely so in Miocene †*scutella*.
2. There is a single suprapygal, not a larger first suprapygal embracing a second suprapygal as in *Homopus* and *Geochelone*.
3. The gulars of each are slightly longer than broad.
4. The single inguinal scute (in Eocene †*comptoni*) is not in contact with the femoral, i.e. is already more specialized than in *Homopus signatus* or *H. boulengeri*.

By itself none of these features is conclusive or diagnostic, but neither does any of them nor any other character positively support relationship of either species to *Homopus*, while at least the presence of the specialized neural pattern in Miocene *scutella* seems to afford a definite negative. There are no grounds for assignment to any other Ethiopian endemic genus. The single suprapygal is unknown in *Geochelone*, the size of which also renders relationship improbable. On the other hand, all characters are consistent with *Testudo sensu stricto*, which is also geographically probable. While, with some hesitation, we refer these European fossils to *Testudo*, it is with full confidence that we exclude them from the ancestry of *Homopus*. Thus *Homopus*, like all other Ethiopian endemics, is at present quite unknown as a fossil.

Remarks. Despite certain emydine-like features, *Homopus*

does not appear to be a primitive genus. Even the seemingly emydine features — relatively depressed shell and transversely developed gulars — are probably as completely secondary as, according to our view, are the unridged maxillae. The anterior neural pattern has departed somewhat from the primitive hexagonal towards a nearly quadrate condition, while the pygal arrangement in *Homopus* is an incipient stage of the advanced pattern. It differs from the typical condition in *Geochelone*,[1] *Gopherus* and †*Stylemys* in that the sulcus between the first vertebral and the supracaudal does not cross the middle of the small second suprapygal; instead it coincides with the suture between suprapygal and pygal.

Hewitt (1931) proposed generically separating *signatus* and *boulengeri* from *Homopus*, under the name of *Pseudomopus*, but later discovered that *Chersobius* Fitzinger (1835) was available. The differences which Hewitt points out are valid, but we do not interpret them as deserving generic recognition. To do so would imply a wider separation and less certainty as to the real affinities of the separated species than, we feel, exists. We regard the species of *Homopus* as forming a single closely-knit series within which are recognizable two species groups: one embracing *signatus* and *boulengeri*, the relatively primitive members of the series, the other comprising the more specialized members — *femoralis* and *areolatus*.

It must be admitted that the skulls of *H. boulengeri* and *areolatus* (Figs. 40, 41) differ appreciably in many ways, but we do not feel that these differences exceed the variation that might be expected within a genus or even within a subgenus. Furthermore, we have not seen skulls of *signatus* or *femoralis* and consequently do not know whether skull structure would group the species in the same way as do external characters such as number of claws and size of inguinals. No very striking skull differences between *signatus* and *boulengeri*, on the one hand, and *femoralis* and *areolatus*, on the other, have been described by Hewitt (1937a), but he mentions differences in skull proportions and other details between *femoralis* and *areolatus*. However, according to him, there does exist in the carpus a species-group difference — the distal carpals of *signatus* and *boulengeri* under-

[1] All subgenera *except* Eocene †*Hadrianus*.

going fusions, while in *femoralis* and *areolatus* they always remain separate.

So far as known, *H. signatus* and *H. boulengeri* are allopatric, *signatus* mainly occurring in northwest Cape Province with a range closely similar to that of *Psammobates tentorius trimeni*, but apparently penetrating farther inland on the plateau (corresponding to climatic region 3a of Finch and Trewortha: 1943.[1] *H. boulengeri* has its principal range in a long inland zone of southern Cape Province, mostly at elevations between 2000 and 3000 feet (approximately climatic region 4b of Finch and Trewortha).[2]

Recent very surprising evidence (Mertens 1955a, see below p. 362 and p. 365) that both *H. signatus* and *H. boulengeri* occur in southern Southwest Africa complicates this apparently simple picture. The ranges of and interrelationships of the two forms in this area are still obscure, however; this is a problem upon which further work is urgently needed.

The nearest recorded points of approach for the two species are Clanwilliam Mtn. (for *signatus*) and Piquetberg (for *boulengeri*) which are about 50 miles apart. We have not seen either of these specimens and cannot state whether there is any approximation of characters in these neighboring populations. Elsewhere, however, the two forms are so distinct that there seems little ground for suspecting intergradation. No other member of the genus displays the characteristic freckled pattern of *signatus*, while *boulengeri* appears to be devoid of pattern though very variable as to shade.

Less obvious, though possibly more significant, is the fact that the normal number of marginals in *H. boulengeri* is 12 pairs — unique as a modal condition among testudinids — while *signatus* has the usual 11 pairs.

H. femoralis and *areolatus* are less distinct, but are said to occur together at Halesowen in the Cradock District. This area of sympatry is very limited as compared with the total range of each species. *H. areolatus* is essentially coastal, extending from Cape Town to Alexandria in southern Cape Province, mostly at low elevations and entering higher ones (above 2000 feet) only where it is said to coexist with *femoralis* (for the most part its

[1] *In* Dudley Stamp: 1953.

[2] Piquetberg itself is at very low elevation (*ca.* 500 ft.) but altitudes up to 3000 ft. from which *boulengeri* may have come, occur in the vicinity.

range coincides with climatic region 5 of Finch and Trewortha). On the other hand, *femoralis* is a creature of the eastern high plateau (roughly climatic region 6 of Finch and Trewortha) mostly occurring at elevations above 3000 feet.

The morphological characters separating these two species are not very striking. They differ in the degree of hooking of the beak, serration of the margin, development of the femoral tubercle, etc., characters which may be entirely valid but which it is easy to imagine being bridged by intermediates. Coloration also differs, but not so impressively as between *signatus* and *boulengeri*.

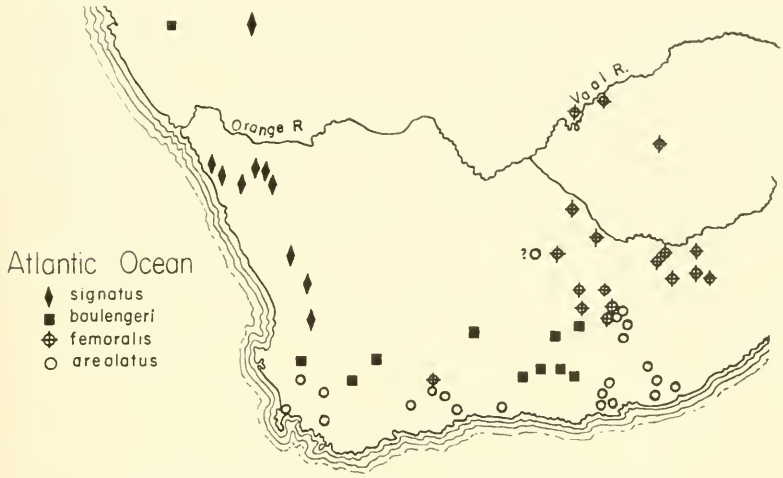


Fig. 38. Distribution of the species of *Homopus* in South Africa.
(P. Washer del.)

We have not seen the specimens from Cradock district identified as *areolatus;* it is somewhat astonishing to find *areolatus* invading the highlands at well over 2000 feet, entering an unusual ecology at just the point where its closest relative occurs! We suggest that the alleged coexistence of *femoralis* and *areolatus* in the district be re-investigated. Cradock specimens (seen by one of us) in the British Museum are clearly *femoralis* but lack the serrate margin mentioned by Boulenger in his original de-

scription of the type. Thus, though Cradock is the type locality of *femoralis,* it is possible that intergradation between *femoralis* and *areolatus* may occur in the area and just to the south of it.

These same two species — *femoralis* and *areolatus* — have also been reported by FitzSimons (1946a:352-353) as occurring together at Welbedacht Farm, Oudtshoorn district. This locality is over 200 miles from any other from which *femoralis* is known. As the identification, apparently correct, is based on a single individual, the possibility of the tortoise having been transported by human agency is worth consideration.

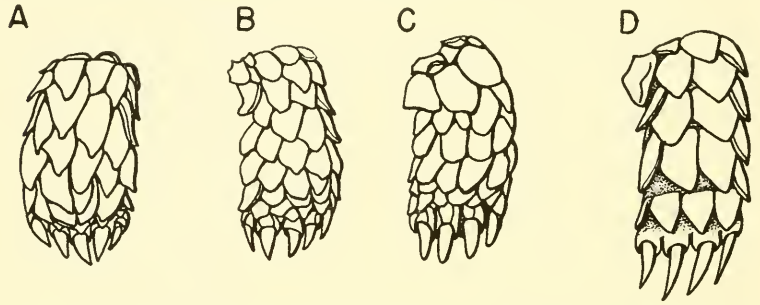


Fig. 39. Forelimb scalation in *Homopus. A, H. signatus* (M.C.Z. 21329); *B, H. boulengeri* (M.C.Z. 42231); *C, H. femoralis* (M.C.Z. 17523); *D, H. areolatus* (M.C.Z. 20967).

(P. Washer del.)

Key to the Species of Homopus[1]

1. Forelimb with 5 claws; inguinal shield single, in contact with the femoral shield 2
   Forelimb with 4 claws; inguinal shields 2-4, small or absent, only the innermost in contact with the femoral shield..... 3
2. Carapace ivory white, yellow or yellowish green, heavily overlaid, spotted or radiated with black; plastron shaded or streaked with brown; posterior margin of carapace in adults usually reverted and serrated; marginals 11-12, usually 11; scutes across forelimb in 5-6 rows. Range:

[1] For *H. bergeri* see *Psammobates t. verroxii,* not a synonym of *boulengeri* as was once suggested.
For *H. darlingi* and *H. nogueyi* see *Kinixys b. belliana* and *K. b. nogueyi* respectively.

Western Cape Province to southern Southwest Africa .....
signatus (Schoepff) (p. 359)

Carapace light olive green, pale yellow, dark yellowish, reddish or blackish brown, uniform or vertebrals edged with brown or black; plastron yellow, dirty green or dark olive, uniform or mesially brown, or each shield edged with brown; posterior margin of carapace not reverted, and not or but slightly serrated; marginals 11-13, usually 12; scutes across forelimb in 3-5 rows. Range: Karroo Plain of south-central Cape Province, South Africa. Also Southwest Africa (see discussion .....*boulengeri* Duerden (p. 362)

3. Carapace olive or brown, uniform or each shield narrowly edged with black; plastron yellow or greenish, uniform or each shield blackish brown anteriorly; posterior margin of carapace more or less reverted and serrated; beak not or but weakly hooked; usually several small scales above nostril; a pair of prefrontal shields; buttock with a very large conical tubercle; heel with conical spurlike tubercle. Range: Eastern Karroo of Cape Province north to western Orange Free State, South Africa .....*femoralis* Boulenger (p. 365)

Carapace yellowish olive, olive or greenish, each shield reddish brown in the centre, the margins edged with dark brown or black; plastron yellowish, mesially brown, rarely uniform; posterior margin of carapace sometimes reverted and not or but slightly serrated; beak strongly hooked; no small scales above nostril; prefrontal usually single or semidivided posteriorly; buttock without a large conical tubercle, at most a flat and inconspicuous one; heel without a conical spurlike tubercle. Range: Cape Province south of 32° S. latitude, South Africa .....*areolatus* (Thunberg) (p. 367)

Homopus signatus (Schoepff)

1782. *Lorica testudinis signatae* Walbaum, Chelonogr. Schildkröten, pp. 71, 120, pl. (which bears an abbreviated form of the name, viz. "Testud. Sign. var."): No locality mentioned.

1792. *Testudo signata* Schoepff, Naturg. Schildkröten, p. 141, pl. xxviii, figs. 2-3; ed. 2, 1801, Hist. Testud., p. 120, pl. xxviii, figs. 2-3). No locality.

1812. Schweigger, 319, 442.

1814. Schweigger, 50.

1831b. Gray, 5.

1831c. Gray, 13.

1836. Bell, text and col. pl.

1865. Strauch, 35.

1872b. Sowerby and Lear, pl. xx (omit text by Gray, cf. *areolatus*).

1802b. *Testudo cafra* Daudin, Hist. Nat. Rept., **2**, p. 291: Kaffraria, Cape Province, South Africa.
1812. Schweigger, 318.
1814. Schweigger, 49.
1820. *Chersine signata* Merrem, 30.
1835. *Homopus*[1] *signatus* Duméril and Bibron, 152.
1849. Smith, A., App., 1.
1870c. Gray, 13 (error).
1872c. Gray (part), 6.
1873b. Gray (part), 15.
1873g. Gray, 320, pl. xii, fig. 1.
1884a. Rochebrune, 15 (in error).
1888d. Boulenger, 136.
1889a. Boulenger, 148.
1890f. Boulenger, 521.
1898. Sclater, W. L., 96.
1905h. Boulenger, 252.
1906c. Duerden, 408.
1907a. Duerden, 10.
1907b. Duerden, 69, fig., pl. vii, figs. 5-6.
1909a. Siebenrock, 514.
1910a. Werner, 299, pl. ix, figs. 13a-b.
1911d. Sternfeld, 48.
1929. Flower, 27.
1955a. Mertens, 34.
1835. *Testudo Chersobius signata* Fitzinger, 122.
1835. *Testudo Chersobius cafra* Fitzinger, 122.
1931. *Pseudomopus signatus* Hewitt, 498.
1934a. Mertens and Müller *in* Rust, 8.
1935. Hewitt, 345.
1935. *Pseudomopus signatus peersi* Hewitt, Rec. Albany Mus., **4**, p. 345, pl. xxxvi: Near Van Rhynsdorp, Klaver District, Cape Province.
1937a. *Chersobius signatus* Hewitt, 791, fig. 3, pl. x, figs. 1-2.
1938. FitzSimons, 155.
1950. FitzSimons, 253.
1950. Rose, 338.

Further citations of "*signatus*" will be found under *Geochelone p. babcocki, Psammobates oculifer* and *H. areolatus.*

[1] *Homopus*, without designated species, was first proposed by Duméril and Bibron in 1834. We have no information as to whether their 1835 volume appeared prior to Fitzinger (1835) in which *Chersobius* was proposed as a subgenus. However, as Fitzinger himself relinquished *Chersobius* in favor of *Homopus* he apparently conceded priority. The matter is discussed by Lindholm (1929:284; footnote 11).

Common Names. Speckled Tortoise (Gray:1844); Marked Tortoise (Gray: 1831b); Walbaum's Tortoise (Flower:1928).

Illustrations. Walbaum's black and white figures of carapace and plastral views are clearly recognizable, Schoepff's and Bell's colored plates less characteristic.

Description. Beak not or but weakly hooked; prefrontal small, divided longitudinally or broken up; frontal small or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with very large, subequal, juxtaposed, strongly imbricate scutes forming 5-6 longitudinal and 6-7 transverse series from elbow to outer claw; claws 5; hinder side of thigh with a very large conical tubercle; claws 4.

Carapace hardly convex, flattened dorsally, sides sloping, scarcely notched in nuchal region, anterior and posterior margins somewhat expanded, reverted, and more or less strongly serrated; dorsal shields concentrically striated with slightly impressed areolae, not swollen, separated by deep grooves, a vertebral keel in the young; nuchal moderate or small, as broad as or broader than long, sometimes divided;[1] notched anteriorly and occasionally posteriorly; vertebrals 5, occasionally 6 or 7, the first about as long as broad, the third to fifth as broad as or broader than long, the fourth and fifth rather broadly in contact, the third narrower than or equal to the third costal; costals 4, sometimes 5, usually not forming an angle with the marginals; marginals 11-12, usually 11; supracaudal undivided.

Front lobe of plastron anteriorly truncate, projecting somewhat at corners, not or but slightly produced, not or but scarcely notched; gulars paired; pectorals moderate, their anterior border straight; axillary 1, moderate; inguinal 1, small or moderate, in contact with the femoral; hind lobe broadly notched posteriorly.

Plastral formula: Abd>h>an>(g, i, p, f, variable, subequal).

Color. In both juvenile and adult the carapace is ivory white, yellow or yellowish green, heavily overlaid, spotted or radiated with black. Plastron ivory white or yellow, more or less heavily shaded with brown or radiating brown lines. Head and neck yellowish, spotted with black above.

Discussed in detail, and extremes figured by Duerden (1907b).

[1] Divided in one Steinkopf specimen (M.C.Z. 42218).

Size. Carapace length of largest ♀ (T.M. 22108) 100 mm., breadth 71.5 mm., height 44 mm.

Habitat. Fairly numerous on granite koppies 16 miles from Bitterfontein.

Localities. Cape Province: Bitterfontein; Clanwilliam Mountain; Grootmist; Kaffraria; Kamaggas; Klipfontein; *Little Namaqualand; O'okiep; Springbok (Springbokfontein); *Steinkopf; Van Rhynsdorp. *Southwest Africa:* Keetmanshoop (Ketmanshoop; *fide* Werner:1910a:300).[1]

Range. South Africa — western Cape Province (chiefly in Little Namaqualand), northwards into southern Southwest Africa.

Erroneously reported from Great Namaqualand by Boettger (1893a) through confusion with *Psammobates oculifer,* also from Rehoboth (Fleck:1894; repeated by Sternfeld:1911b); see Mertens (1955a:34). Also in error from Abyssinia and Mauritius (Gray:1844), and Senegambia (Rochebrune:1884a).

Homopus boulengeri Duerden

1906c. *Homopus boulengeri* Duerden, Rec. Albany Mus., 1, p. 406, pl. xi, figs. 1, 2 and 5: Willowmore; Aberdeen; and Beaufort West Districts, Cape Province, Union of South Africa.
1907a. Duerden, 10.
1907b. Duerden, 67, fig., pl. vi, fig. 1.
1909a. Siebenrock, 515.
1910. Siebenrock, 697, pls. i and iii.
1955a. Mertens, 33.
1934a. *Pseudomopus boulengeri* Mertens and Müller *in* Rust, 8.
1935. Hewitt, 345.
1946a. FitzSimons, 353.
1950. FitzSimons, 253.
1950. *Chersobius boulengeri* Rose, 338.

Synonymy. Homopus bergeri Lindholm was erroneously synonymized with *H. boulengeri* by Siebenrock (1909a:515); actually it is a synonym of *Psammobates tentorius verroxii.*

Common names. Donner-weer (local name, since it appears after thunderstorms: Hewitt).

Illustrations. Duerden (1906c) supplies rather indistinct

[1] Mertens (1955a) confirms the presence of this species in Southwest Africa but his specimens are without exact locality.

photos of the plastral and lateral view of a cotype, also figure of head; later (1907b) a dorso-lateral photograph. Siebenrock (1910) also presents dorso-lateral and plastron photos, besides clear pictures of the head, forearm and egg.

Description. Beak not or but moderately or strongly[1] hooked, bicuspid[2] or tricuspid;[1] prefrontal small, divided longitudinally, usually preceded by a small median and two lateral shields of nearly the same size as the prefrontals; frontal broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with extremely large, subequal, juxtaposed,

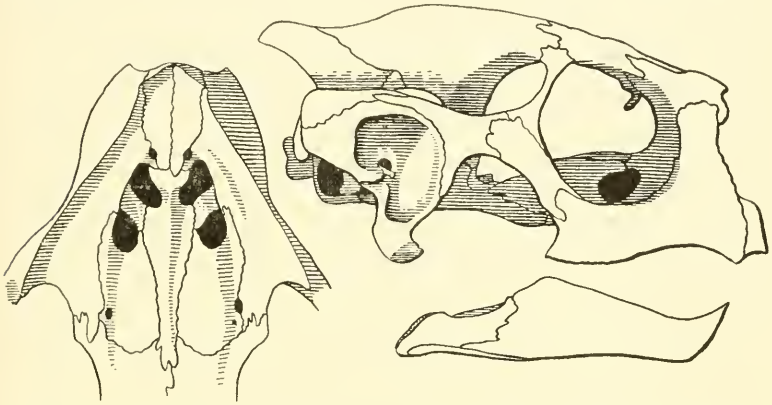


Fig. 40. Skull of *Homopus boulengeri* (A.M.N.H. 7109). Condylobasal length 22 mm.

(S. McDowell del.)

strongly imbricate scutes forming 3-5 longitudinal and 8 transverse series from elbow to outer claw; claws 5; hinder side of thigh with, or rarely without, a large conical tubercle; heel of ♂ surrounded by smaller tubercles but without definite spurlike tubercle; claws 4, rarely 5; tail without terminal clawlike tubercle.

Carapace scarcely convex, flattened dorsally, sides sloping, scarcely notched in nuchal region, anterior and posterior margins expanded, not or but slightly reverted, not or but slightly ser-

[1] Strongly *fide* Duerden.

[2] In S.M. 49822 from Plateau Farm, near Aus, Southwest Africa.

rated; dorsal shields concentrically striated, the areolae not impressed,[1] not swollen, separated by deep grooves; nuchal small, as long as or slightly longer than broad; vertebrals 5, broader or much broader than long, as broad as or narrower than the costals, the fourth and fifth rather broadly in contact; costals 4, not forming an angle with the marginals; marginals 11-13, usually 12; supracaudal undivided.

Front lobe of plastron anteriorly truncate, projecting somewhat at corners, not or but slightly produced, not or but slightly notched; gulars paired; pectorals moderate, their anterior border somewhat sloping, widening slightly towards the axillary notch; axillary 1, moderate; inguinal 1, moderate or large, in contact with the femoral; hind lobe broadly notched posteriorly.[2]

Plastral formula: Abd>h>(g, p, f, and an, variable).

Color. Carapace dark reddish or yellowish brown, or light olive green, uniform (in young) or the vertebral shields edged with bright brown or black. Plastron yellow, dirty green or dark olive, uniform or mesially brown, or each shield edged with brown. Jaws brown, head and limbs light olive green. In life the naked parts of skin are said to be bright yellow with minute orange scales.

Size. Carapace length of Duerden's largest cotype 105 mm. Carapace length of largest ♂ (T.M. 19177), 108 mm., breadth 74.5 mm., height 48.5 mm. Carapace length of largest ♀ (T.M. 19838), 110 mm., breadth 80 mm., height 49.5 mm.

Sexual dimorphism. Plastron of ♂ ♂ deeply concave posteriorly, not in ♀ ♀; hind lobe of plastron deeply notched in ♂ ♂, more open in ♀ ♀ (Duerden).

The relatively small size of the posterior aperture of the ♀ shell opening — 6 mm. long by 15 mm. broad in one specimen — in relation to the large size of the egg, is referred to by Siebenrock (1910) who suggests that during deposition of the egg significant widening of the aperture must take place. This could be achieved by a spontaneous mobility of the posterior lobe of the plastron, which, he says, has been demonstrated to occur in *Pyxis arachnoides* (cf. Siebenrock:1906b) and in *Testudo s. str.*

Breeding. The egg referred to and figured by Siebenrock (*vide*

[1] Moderately or deeply according to Duerden (1906c:406).

[2] In S.M. 49822 from Plateau Farm, near Aus, Southwest Africa.

supra) measured 22 x 39 mm. The poles were strikingly pointed and it was hard-shelled when removed from the oviduct. As there were no other mature eggs, Siebenrock suggests that only one is produced at a laying.

Localities. Cape Province: Aberdeen district; Beaufort West district; *Cape Province; Hoek-onder-Berg Farm between Montague and Touws River; Matjesfontein; Miller Station, Klipplaats between Aberdeen and Willowmore; Pearston district; Piquetberg; Willowmore; Zwart Ruggens, Aberdeen district. *Southwest Africa:* near Aus.[1]

Range. South Africa — restricted to the Karroo Plain area of south central Cape Province; and apparently Southwest Africa near Aus.[1]

Though its range is not so restricted as Duerden (1906c) assumed, he is apparently correct in saying that no other *Homopus* occurs in its habitat.

Homopus femoralis Boulenger

1888g. *Homopus femoralis* Boulenger, Proc. Zool. Soc. London, p. 251, pl. xiv: Cradock, Cape Province, Union of South Africa.
1889a. Boulenger, 147.
1890f. Boulenger, 521.
1890. Strauch, 58.
1898. Johnston, 361 (in error).
1898. Sclater, W. L., 96.
1906c. Duerden, 407, pl. xi, fig. 6.
1907a. Duerden, 10.
1907b. Duerden, 67, fig., pl. vi, fig. 2, pl. viii, fig. 9.
1909a. Siebenrock, 514.
1929. Flower, 27.
1931. Hewitt, 496, fig. 4a.
1934a. Mertens and Müller *in* Rust, 8.
1937a. Hewitt, 788, 791, 795, pl. x, fig. 3.
1937e. Hewitt, 10, pl. ivA.
1946a. FitzSimons, 353.
1950. Rose, 336.

[1] Mertens (1955a:33) received a living pair (♂, ♀) [one of which we have examined] from Plateau Farm near Aus, Southwest Africa (H. Erni donor). This astonishing record is so far removed from the generally accepted range that we specially asked Dr. Mertens about it. He replied that, though he did not collect them himself, he has every confidence in the collector and, furthermore, that during his trip he heard reports of the occurrence of a strongly-flattened, rock-dwelling tortoise in the southern portion of Southwest Africa.

Common names. Karroo Tortoise or Greater Padloper (Hewitt); Boulenger's Tortoise (Flower); *Padlopertjie* (Afrikaans, A. C. Hoffman *in litt.*).

Illustrations. Boulenger's (1888g) figure of the type is in color.

Description. Beak not or but weakly hooked, tricuspid, edge of jaws serrate; a few small scales above the tubular nostrils; prefrontal large, divided longitudinally; frontal large or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with a few extremely large, subequal, juxtaposed, strongly imbricate, pointed scutes forming 3-4 longitudinal and 7-8 transverse series from elbow to outer claw; claws 4; hinder side of thigh with a very large conical tubercle; heel with large, conical, spurlike tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace somewhat convex, flattened dorsally, sides sloping, not or but scarcely notched in nuchal region, anterior and posterior margins somewhat expanded, more or less reverted, and more or less strongly serrated; dorsal shields concentrically striated with slightly impressed areolae divided by a weak keel, not swollen, convex; nuchal elongate, subtriangular or slightly longer than broad; vertebrals 5, the first as long as or longer than broad, the second to fifth broader than long, the fourth and fifth somewhat narrowly in contact, vertebrals two and three narrower than the costals; costals 4, not forming an angle with the marginals; marginals 11; supracaudal undivided.

Front lobe of plastron anteriorly truncate, not produced, scarcely notched; gulars paired; pectorals very narrow, their anterior border widening abruptly towards the axillary notch; axillary 1; inguinals 2 or 3, the outermost triangular, the others transverse, the innermost in contact with the femoral; hind lobe broadly notched posteriorly.

Plastral formula: Abd>h>an>or<f>or=g>or=p. Pectoral is typically the shortest scute.

Color. Carapace olive or brown, pale or dark, with or without a dull red or orange tinge, each shield narrowly edged with black (in young) or uniform (in adult). Plastron yellowish or greenish, each shield blackish brown anteriorly (in young, but sometimes persists), or uniform (adult). The shielded or tuber-

culate soft parts yellow or pale brownish, the naked areas tinged with salmon or orange. See also discussion in Duerden (1907b: 67).

Size. Carapace length of largest ♂, 133 mm., breadth 102 mm. Carapace length of largest ♀, 157 mm., breadth 121 mm. (both Hewitt:1937c, but no localities mentioned).

Sexual dimorphism. The plastron is flat in both sexes, but the ♂ supracaudal is usually larger and directed downwards.

Breeding. The eggs are oval to nearly spherical, ranging from 25 x 29 mm. to 25 x 33 mm., and quite soft when deposited (Hewitt:1937c:11).

Diet. Bulbine caulescens is a favorite food (P. M. Niven in Hewitt:1937c).

Enemies. See under *areolatus.*

Habitat. Grassveld up to 5,500 feet.

Localities. Cape Province: Aliwal North; Barkly West; Colesberg; Cradock; Dordrecht; Halesowen; Indwe; Lady Grey; Middleburg; New Bethesda; *Philipstown; Sneeuwberg; Stormberg; Warrenton; Welbedacht Farm, Oudtshoorn district;[1] Wodehouse=Dordrecht. *Orange Free State:* Bloemfontein[2] (specimen in Senckenberg Museum seen by E. E. W.).

Range. South Africa — eastern Karroo of Cape Province north to western Orange Free State.

Erroneously reported from British Central Africa by Johnston (1898).

Homopus areolatus (Thunberg)

1787. *Testudo areolata* Thunberg, Kongl. Vetensk, Akad. Handl., **8**, p. 181, fig.: "India" (in error).
1792. Schneider, 267.
1792. Schoepff, 121, pl. xxiii.
1795. Schoepff, 104, pl. xxiii.
1802b. Daudin, 287.
1812. Schweigger, 320, 443 (omit localities).
1814. Schweigger, 51.
1831b. Gray, 5.
1831c. Gray, 13.

[1] See p. 358 for comments regarding this record.

[2] Dr. A. C. Hoffman, Director of the National Museum in Bloemfontein, sees no reason to question this record as *femoralis* is "very plentiful" and "occurs in practically every district of the Free State." (*in litt.*)

1835. Temminck and Schlegel, 73.
1836. Bell, text and col. pl. —.
1862a. Strauch, 92.
1865. Strauch, 35.
1872b. Gray, 5, *in* Sowerby and Lear, pl. xxi.
1880c. Vaillant, 34, 88.
1887b. Boettger, 140.
1890. Müller, F., 705.
1890. Strauch (part), 58.
1788. *La Vermillon* Lacépède, Hist. nat. Quadrup. ovip. Serpents, 1. p. 166, and *Testudo miniata* in Synopsis Methodica, a table at end of same volume in which binomials are employed: Cape of Good Hope.
1802b. *Testudo pusilla* Daudin (not of Linnaeus), 299.
1804. *Testudo* (*Africana*) Hermann, Observ. Zool. Animal. Spec., p. 218: No locality.
1820. *Chersine areolata* Merrem, 30.
1829. Gravenhorst, 18.
1820. *Chersine tetradactyla* Merrem, Vers. Syst. Amphib., p. 32: "India orientali" (in error).
1831c. *Testudo areolata* var. *pallida* Gray, Synopsis Reptilium, p. 13: South Africa.
1855. Gray, 12.
1835. *Homopus areolatus* Duméril and Bibron, 146.
1844. Gray, 10.
1845b. Rüppell, 297.
1849. Smith, A., App., 1.
1855. Gray, 11.
1857. Jan, 35 (as *Homoeopus*).
1860. Fitzinger, 411.
1867a. Steindachner, 4.
1873b. Gray, 15.
1873c. Gray, 726, pl. lx, fig. 5.
1884a. Rochebrune, 16 (in error).
1885. Smets, 10 (locality erroneous).
1889a. Boulenger, 147.
1890f. Boulenger, 521.
1893a. Boettger, 8.
1895. Oudemans, 321.
1898. Jeude, 5.
1898. Johnston, 361 (in error).
1898. Sclater, W. L., 96.
1903e. Boulenger, 217.
1904b. Tornier, 209, 303, fig. 11.

1906c. Duerden, 407, pl. xi, fig. 4.
1907a. Duerden, 9.
1907b. Duerden, 68, fig. —, pl. vi, fig. 3.
1907j. Boulenger, 482.
1909a. Siebenrock, 513.
1910. Siebenrock, 695.
1925b. Flower, 924.
1928. Cott, 952.
1929. Flower, 26.
1929. Rose, 188, 231, fig. 124.
1931. Hewitt, 496, figs. 4b-4c.
1934a. Mertens and Müller *in* Rust, 8.
1937a. Hewitt, 790, fig. 4, pl. x, fig. 4.
1937e. Hewitt, 9, pl. ii, fig. 4; pl. iv, fig. 2.
1946a. FitzSimons, 352.
1950. Rose, 336, fig. 202.
1950. Williams, 551.
1844. *Homopus signatus* Gray (not of Schoepff), 10.
1855. Gray, 11.
1872c. Gray (part), 6.
1873b. Gray (part), 15.
1872b. *Testudo signatus* Gray (not of Schoepff), 5 (text: *not* pl.).

A further reference to "*Testudo areolata*" will be found under *Kinixys b. belliana.*

Synonymy. Testudo miniata, which Lacépède called "La Vermillon" in allusion to the reddish tinge of its protuberant snout, was first referred to the synonymy of *areolatus* by Bell (1836). *Testudo africana* Hermann is placed in the synonymy of *areolatus* by us on account of its depressed shell, short gulars, and coloration. *Testudo fasciata* Daudin (1802b), heretofore generally regarded as a synonym of *areolatus,* we reject because the type was stated to have had five claws on either forefoot. It is also said to have come from Ceylon.

Common names. Parrot-beaked Tortoise (Hewitt:1937e) would appear preferable to either Areolated Tortoise (Gray:1831b), Thunberg's Tortoise (Flower:1929), or Grooved Tortoise (Rose: 1929), the latter having long been used for *Geochelone sulcata. Padloper* in Afrikaans, on account of their tendency to keep to paths or roads (C. J. Latrobe:1818).

Illustrations. Schoepff's (1792) plates supply dorsal, plastral and lateral views in color. Bell's (1836), reproduced in Sow-

erby and Lear (1872), show the entire animal, including its plastral aspect, in color.

Description. Beak strongly hooked, tricuspid, edge of jaws anteriorly weakly serrate; no small scales above tubular nostrils; prefrontal large, single or posteriorly semi- or wholly divided longitudinally; frontal moderate or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with extremely large, subequal, juxtaposed, strongly imbricate, pointed scutes forming 3-4 longitudinal and 6-8 transverse series from elbow to outer claw; claws 4; hinder side of thigh with or without (irrespective of sex) a slightly enlarged, low and incon-

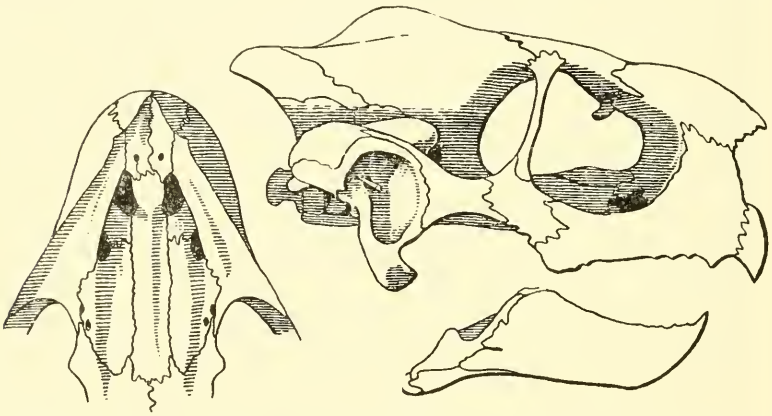


Fig. 41. Skull of *Homopus areolatus* (A.M.N.H. 17792). Condylobasal length 21 mm.

(S. McDowell del.)

spicuous tubercle; heel without definite spurlike tubercle; claws 4; tail without terminal clawlike tubercle.

Carapace moderately convex, more or less flattened dorsally, sides sloping, scarcely notched in nuchal region, anterior margin not or but slightly expanded, posterior margin not expanded, sometimes reverted, and not or but scarcely serrated; dorsal shields concentrically striated, with impressed areolae sometimes showing a longitudinal keel, more or less swollen, separated by grooves; nuchal variable, elongate, subtriangular or quadrate;

vertebrals 5, rarely 4,[1] 6[2] or 8,[3] scarcely convex, the first and fourth longer than broad or (rarely) as long as broad, the second, third and fifth broader than long, the fourth and fifth only narrowly in contact, the third as broad as, though usually narrower than, the third costal; costals 4, rarely 5,[4] not forming an angle with the marginals; marginals 11, rarely 10, 12[5] or 13; supracaudal undivided, rarely divided.[6]

Front lobe of plastron anteriorly truncate, not produced, not or but scarcely notched; gulars paired, small but broad; pectorals somewhat narrowed, their anterior border steeply sloping and widening abruptly towards the axillary notch; axillaries usually 1 or 2, sometimes 3 or 4, even 5,[7] the inner small, the outer moderate; inguinals 3 or 4, rarely absent,[8] or only the outermost present, outermost triangular, the rest transverse, the innermost in contact with the femoral; hind lobe broadly notched posteriorly.

Plastral formula: Usually Abd>h>an>(g, p, f subequal). F>an in a Grahamstown specimen (M.C.Z. 17524). The femoral suture is always smaller than that of the anal, according to Hewitt (1931:498).

Color. Carapace yellowish olive, olive or greenish, each shield reddish brown in the centre, the margins edged with dark brown or black. Plastron yellowish, mesially brownish, rarely uniform.

According to Siebenrock (1910:697) the ♂ ♂ are much more lightly colored than the ♀ ♀, especially the plastrons which in ♂ ♂ are mostly uniform, while those of the ♀ ♀ are almost always more or less darkly pigmented; the young of the two sexes are indistinguishable. Duerden (1907b:68) remarks that tortoises from around Cape Town are usually darker than those from eastern Cape Province. For detailed descriptions of the color of live specimens see Bell (1836).

[1] Four in a specimen mentioned by Oudemans (1895).

[2] Six in a tortoise figured by Schoepff (1792: pl. xxiii), also in one mentioned by Bell (1836).

[3] Eight in a specimen figured by Gottwald (pl. K, fig. 14) *fide* Strauch (1862a).

[4] Five in one mentioned by Bell (1836), and in two of Oudemans (1895).

[5] Twelve in a specimen (U.S.N.M. 131846) without data.

[6] Divided in one of Oudemans' (1895) series from Knysna and Port Elizabeth.

[7] Five occasionally according to Hewitt (1931:499).

[8] Absent in a Knysna tortoise (M.C.Z. 20967) only, but Siebenrock (1910) alleges that they are frequently absent.

Size. Carapace length of largest ♂, presumably from Knysna, 96 mm. (Oudemans:1895); another ♂ (M.C.Z. 21457) from Table Mountain, has a carapace length of 95 mm., breadth 67 mm., height 39.5 mm.

Carapace length of largest ♀, a Grahamstown specimen (Hewitt:1937e), 114 mm., breadth 86 mm.; another Grahamstown ♀ (M.C.Z. 22474), has a carapace length of 107 mm., breadth 82 mm., and height 53 mm.

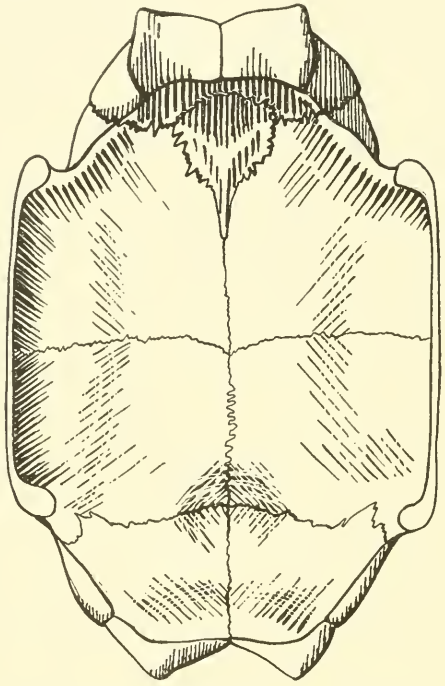


Fig. 42. Internal view of plastron of *Homopus areolatus* (B.M. 64.11.20. 15), x 1.

(P. Washer del.)

Sexual dimorphism. Judging by the material available to us, Siebenrock's (1910:697) conclusion regarding sexual differences in the plastral coloring of adults (*vide supra*) is not quite accurate. We are not in a position to verify other alleged

distinctions that he cites. Both Boulenger (1890f) and Oudemans (1895) present charts of secondary sexual characters, the former stating that ♂ ♂ have larger heads, longer and more pointed snouts, longer mandibular symphyses, and a larger elbow scute. Oudemans failed to note any appreciable sexual difference in size of elbow scute, but concurs as to the validity of the cranial characters cited by Boulenger if restricted to specimens with a carapace length of over 90 mm. Oudemans failed to find the horny terminal tubercle which Boulenger observed on the tail of one of his specimens, but notes that the tails of ♂ ♂ are somewhat longer. Oudemans comments on the absence of any concavity in the plastrons of his ♂ ♂ ; and in our material at most only a very slight central depression is discernible, the plastron being practically flat in both sexes.

Breeding. Nest holes are about 3 inches deep. The eggs, from 2 to 5, possibly averaging 3 at a laying, are elongate ovals ranging from 21 x 27 to 23 x 33 mm. (Hewitt:1937a; pl. xxvii: fig. 8). Incubation takes 7 to 8 months, *fide* Rose (1950:337).

Longevity. Three years, 1 months, 10 days in the London Zoo, but usually die within one year of arrival (Flower:1925b).

Diet. The only information is indirect: it is said not to be destructive in gardens or on farms (Hewitt:1937e).

Parasites. A tick is present on one of the M.C.Z. series.

Enemies. Jackals prey on the young whose shells are easily cracked. One "*Homopus,*" together with 23 other reptiles, was recovered from the stomach of a ♀ Secretary Bird (*Sagittarius serpentarius*) shot on the Cape Flats (Stark and Selatan, Birds of South Africa, **3**:405). Other birds of prey, according to Kolbe as quoted by Lacépède and others, carry them up and drop them on the rocks to break their shells. Crows, on the other hand, turn them over and with their strong beaks attack the softer parts, pecking out the edible portions (Latrobe:1818).

Defense. The head is incompletely protected when it and the forelimbs are withdrawn inside the shell (Hewitt:1937e:10).

Temperament. Readily tamed according to Bell (1836) who found they would take food from one hand while being held in the other. A fairly bold and active tortoise that struggles violently with outstretched head and limbs when picked up (Hewitt:1937e:10).

Habitat. The only *Homopus* species occurring on the Cape Peninsula (Rose:1929). A shade-loving tortoise inhabiting the sour-grass areas from sea-level to the summit of the Zuurberg (Hewitt:1937e:9).

Localities. Cape Province: Albany district; Alexandria district; Bathurst district; Cape Peninsula; Deelfontein;[1] De Wet; *Dunghye Park, Caledon; Garcia; Glen Epstine (as Erskine in Hewitt:1937e), Cradock district; *Grahamstown (including Carlisle Bridge; Mountain Drive and Gunfire Hill); Halesowen; *Kenkelbosch (seen at U.S.N.M.); Knysna; Malmsbury; Mortimer; Oudtshoorn; Pigott Bridge; Port Elizabeth; Simons Bay Mountains; *Table Mountain; *Tootabi near Alicedale; Uitenhage; Welbedacht Farm, Oudtshoorn district; Zuurberg.

Range. Cape Province south of 32° S. lat. (except for Deelfontein record[1]), Union of South Africa.

Erroneously reported from India (Thunberg); Matabeleland and Zambezi region (Smets); British Central Africa (Johnston); Victoria Nyanza (Stranch and Siebenrock); Senegambia (Roehebrune).

Genus KINIXYS Bell

1827. *Kinixys* Bell, Trans. Linn. Soc. London, **15**, p. 398. Type: *castanea* Bell = *Testudo erosa* Schweigger (by original designation).

1835. *Cinothorax* Fitzinger, Ann. Wiener Mus., **1**, pp. 108, 111, 121. Type: *Kinixys belliana* Gray (designation by Fitzinger: 1843).

1843. *Cinixys* Fitzinger, Syst. Rept., p. 29 (emendation of *Kinixys* Bell).

1873b. *Kinothorax* Gray, Hand-List Shield Rept. Brit. Mus., p. 16 (emendation of *Cinothorax* Fitzinger).

Definition. Skull with triturating surfaces of maxilla and premaxilla without ridges; maxillary not entering roof of palate; anterior palatine foramina large, conspicuous; prootic well exposed dorsally; quadrate enclosing stapes; surangular subequal in height to prearticular; neck with third centrum biconvex.

Carapace of adult movable posteriorly, usually hinged between the fourth and fifth pleurals (costal bones) and seventh and eighth peripherals (marginal bones); outer side of third costal scute shorter than that of fourth; anterior neurals hexa-

[1] The Deelfontein record requires investigation and verification.

gonal; submarginal scutes present; suprapygals 1 or 2, if 2 typically separated by a straight transverse suture.

Plastron not hinged; gular region greatly thickened and produced; gular shields paired, longer than broad.

Distinguishing marks. The distinctive carapacial hinge sufficiently differentiates adult members of this genus. Young *Kinixys,* prior to development of the hinge, may be recognized by the relationship between third and fourth costal shields as defined above (see Fig. 13), and also by the presence of the submarginal scute, though this may be difficult to see.

Range. Africa from 17° North, south to Bechuanaland and Natal. Madagascar (? introduced).

Fossil record. None.

Remarks. In view of the many remarkable characters distinguishing *Kinixys* — some from all, others from the majority of tortoises — it is not surprising that the genus was separated at an early date and its status never since questioned. However, well differentiated though it is, *Kinixys* is not an isolated genus. Below, we cite special resemblances to single genera among the Ethiopian endemics, while in a previous section we have argued for the phyletic unity of an Ethiopian group that includes *Kinixys.*

Adult members of the genus *Kinixys* are recognizable by the unique hinging of the carapace, but as hinging is ontogenetically a late phenomenon, and one that may sometimes fail to develop both in *Kinixys* and *Testudo* (*vide infra*), it is not fully satisfactory for generic definition. Startling though the hinge of *Kinixys* may be, hinging is a recurrent phenomenon among testudinates, an adaptation to which their solid armor is especially suited. It has occurred once in the Pelomedusidae, once in the Kinosterninae, four times independently in the Emydinae, three times independently in the Testudininae. In many of these instances species with or without hinging are obviously closely related.

The three examples of hinging in the Testudininae all differ, not only from one another, but also from the type of hinging that occurs repeatedly among emydines. In emydines the plastron is hinged between the hyo- and hypoplastron at the junction of pectoral and abdominal scutes. In *Kinixys,* as al-

ready mentioned, the hinge is carapacial. In *Pyxis* it occurs far forward on the anterior lobe of the plastron and, as shown by Siebenrock (1906b), tends to involve a break across the entoplastron. In *Testudo,* when present, the hinge is at the base of the posterior lobe where the abdominal scutes contact the femoral, and so involves the hypo- and xiphiplastron. In *Testudo sensu stricto* it may be present in one sex of a species and absent in the other, so that the presence or absence of a hinge cannot be considered as automatically implying generic rank. It is not on account of its hinge that we have retained *Kinixys* as a genus, but because of the complex of characters that indicate a long period of separation and divergence from all related lines.

The hinging of the dorsal shell in *Kinixys* involves the backbone also. The morphology of this peculiar condition has been discussed in some detail by Siebenrock (1907). It is an entirely secondary condition that gradually develops with age. The interdigitating sutures originally present between the seventh and eighth marginals (besides the numerically corresponding peripherals), together with the second and third costal shields (also fourth and fifth pleurals), disappear with maturity as fibrous cartilage intervenes between the now smooth edges of these elements. The hinge first forms peripherally and spreads inward; as a final step the transverse suture between the fourth and fifth neurals is loosened.[1]

There is some evidence that this ontogenetic process occasionally fails to continue to completion. At least, various authors (Müller; Hewitt, etc.) have described apparently mature specimens of *K. b. belliana* in which the dorsal hinge was so poorly developed as to be immovable, or almost so.

Though the hinge is fully formed only in mature members of the genus and is totally absent in hatchlings, a preparatory modification in hatchlings is shown by the shapes of the third and fourth costals: the third being narrowed distally and the fourth correspondingly widened. Furthermore, the fourth costal, contrary to the general rule among turtles, may be substantially greater in area than the third.

This dorsal scute modification appears to be the most constant

[1] According to Siebenrock (1907) the fifth neural is somewhat displaced, moving forward above the fourth so as to permit of increased mobility. We have been unable to confirm this.

external character by which juvenile *Kinixys* may be recognized. The presence of the so-called "submarginals" of Siebenrock — one or more supernumerary scutes internal to the ventral surface of the second marginal — is also diagnostic of the genus, but these vary much in size and are not always easily visible.

Osteologically, there are various features unconnected with the hinge that make *Kinixys* a specially distinctive genus — though some of these features are shared with one or another related genus. One minor point is the position of the costomar-

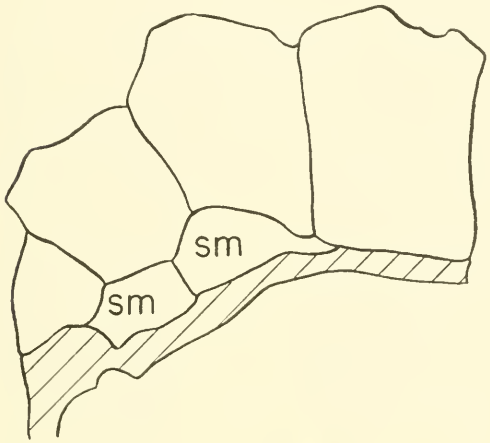


Fig. 43. *Kinixys erosa* (Yale Mus. 5403) (x ⅔). Internal view of left anterior edge of carapace; *sm* = submarginal scale.

(P. Washer del.)

ginal sulcus with reference to the pleuroperipheral suture. Whereas in tortoises generally there is complete, or almost complete, congruence between these two landmarks, in *Kinixys* the costomarginal sulcus is, at least on the posterior half of the shell, well down on the peripherals. In this respect *Pyxis* and *Acinixys* are somewhat like *Kinixys,* and the feature is probably an emydine inheritance, as is also the case with the position of the vertebral-supracaudal sulcus on the pygal in *Kinixys* (well down on the pygal in *K. erosa* and *homeana,* higher in *belliana*).

Another peculiarity, shared with *Chersina* however, is

the anteroposterior lengthening of the anterior peripherals, the anteroposterior length of the second peripheral being greater than the anteroposterior length of the first pleural. Also rather unusual in a tortoise is the nearly complete absence of differentiation among the pleurals by alternate widening and narrowing.

In *Kinixys* the gular region of the plastron is strikingly modified by hypertrophy of the epiplastral lip. A tendency to develop a thickened epiplastral lip, recessed behind, exists in all tortoises. It is weakest in *Homopus, Malacochersus* and some *Testudo*, such a thickened lip apparently being one of the many testudinate characters displaying parallel development. Its significance is obscure, especially so in the present case in which, as Boulenger (1889a:142) has noticed, the length of the thickened portion may be appreciably more than a fourth of the total length of the plastron. In this respect no other tortoises approach *Kinixys* except *Chersina,* in which the very similar hypertrophy of the epiplastral lip may even exceed the development shown in some *Kinixys* (cf. Figs. 37B and 49).

Among continental African genera the skull of *Kinixys* is distinctive in its pointed snout, as seen from above. This character is discernible in hatchlings and led to further examination and re-identification of the desiccated juvenile from the Rondo Plateau mistakenly assigned to *Malacochersus tornieri* by Loveridge (1942c:248). However a similarly pointed snout is present in *Pyxis* of Madagascar.

According to Hewitt (1937a:791) another characteristic of *Kinixys* is the lack of fusion of the distal carpals. Such fusion is usual in *Geochelone, Testudo* and *Psammobates.* It occurs also in *Homopus signatus* and *boulengeri* but is absent in *H. femoralis* and *areolatus* (*fide* Hewitt:1937a). It is also lacking in two British Museum specimens of *Chersina* examined by one of us (E.E.W.). However, according to Siebenrock (1906b) this is a purely individual character without taxonomic significance. The matter requires re-examining with more adequate material.

Species groups. It has been suggested (for example by Schmidt: 1919) that *belliana* should be removed from *Kinixys*, the type of which is *erosa*, and placed in the genus *Cinothorax* Fitzinger. However, *homeana* so clearly bridges the gap between

erosa and *belliana* that we can see no advantage in the recognition of *Cinothorax* either as genus or subgenus. This natural grouping is sufficiently indicated in less formal fashion by describing (as much on the ground of ecology as structure) two species groups within the genus, one with the two rain-forest species, *K. erosa* and *K. homeana,* the other with only the savanna form *K. belliana.*

Kinixys belliana, the best known species, occurs over a vast area of African savanna (climatic region 2 of Finch and Trewartha) and borders in a great arc on three sides the range of the other two members of the genus. Both in habitus and coloration it dis-

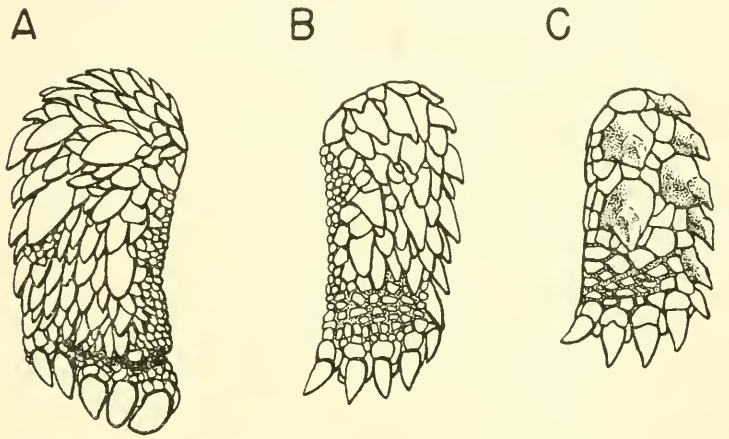


Fig. 44. Forelimb scalation in *Kinixys,* (all x 1). *A, K. b. belliana* (M.C.Z. 41945); *B, K. homeana* (M.C.Z. 38371); *C, K. erosa* (M.C.Z. 22486).

(P. Washer del.)

plays great variability. At times these differences are individual, at others they appear to characterize populations, and consequently have resulted in the proposal of numerous species and subspecies. All but one of these we reject as not being sufficiently distinct, either morphologically or geographically. The name *spekii* Gray is an example. One of us (A.L.) has used it on several occasions, but when the species *belliana* was considered as a whole we did not find it possible to retain *spekii,* except in a very

subjective and geographically meaningless way. A subspecies based on this name would have neither range nor boundaries; it would more easily be applicable to individuals than to populations; it would in fact be a morphologieal type rather than a geographically differentiated segment of the species. On the available evidence we level this same criticism at the majority of the proposed subspecies of *belliana*.

We are conscious that we may have undervalued some segment (perhaps, for example, *K. spekii*, which was originally described as a full species) of what appears to us, on the available evidence, as one highly variable species. There are obviously characters worthy of study which require better analysis than we have been able to give them. An example is the condition of the postorbital bone. In the material studied by us the postorbital bone may be *absent*, or a *loose* thin bar of bone, or a thin bar of bone *solidly sutured* to the frontal above and the jugal below. However, we have not had material to check in adequate fashion the correla-

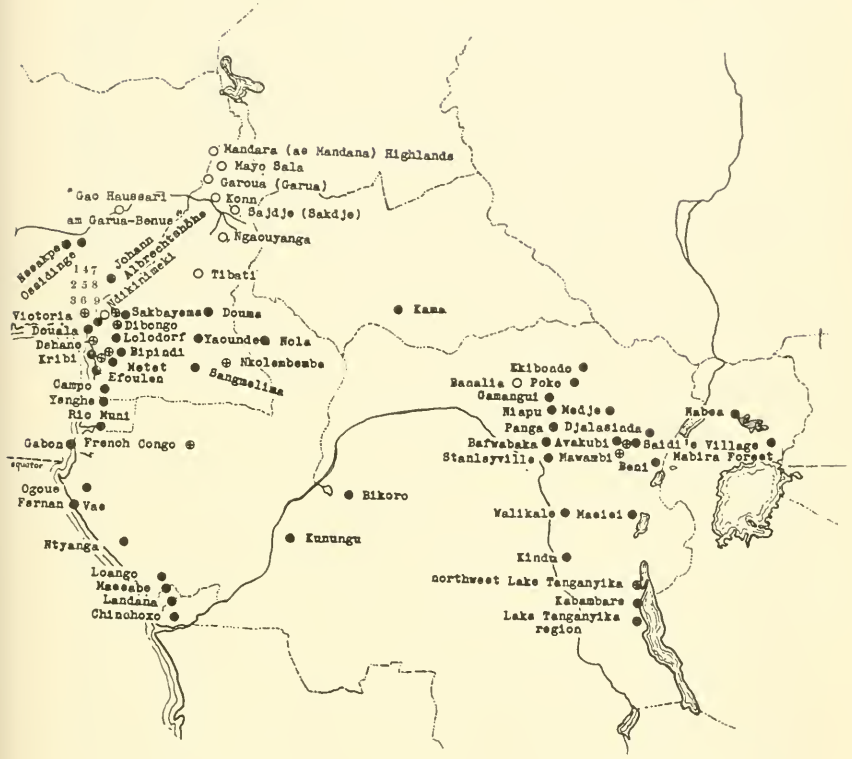


Fig. 45. Locality records of *Kinixys* (exclusive of *K. b. belliana* whose range extends from the Cameroon east and south). Other *erosa* localities encircle Cameroon Mountain, (4), viz. Bonge (1) and Buea (5); with *homeana* recorded from Bibundi (2); Isongo (3); Mpanga (6); Mujuka (7); Mosake (8) and Likomba (9).

(P. Washer del.)

tion of these three conditions with other characters and with geography. We have therefore been conservative in our taxonomic approach. We agree with Hewitt (1931:466) who, while thinking "that a number of allied species and subspecies can be recognized" among what is here called *belliana,* admitted that "the data for sharply defining them are *not yet available.*" (Italics ours.)

The only subspecies of *belliana* that we have retained is *nogueyi* Lataste. It is distinguished by having lost a claw on each forefoot, a condition correlated with a definable range within which it is constant so far as our evidence goes. Though the character of a 4-clawed forefoot is pure in the populations we call *nogueyi,* it crops up occasionally within the range of what we call *b. belliana.* This fact, first noticed in a juvenile from Beira by Boulenger, induced both him and Siebenrock to synonymize *nogueyi.* However, the overwhelming predominance of 5-clawed forefeet throughout the range of *b. belliana* affords ample justification for the retention of *nogueyi* as a western race.

The other ecological species group consists of *K. homeana* and *crosa* which are restricted to the rain forests of West and Central Africa (climatic region 1 of Finch and Trewortha). Morphologically, all three species are readily identifiable, as may be seen by reference to Table 7 on p. 383. As indicated there, *K. homeana* and *crosa,* which occur together in at least a macrogeographic sense, agree in coloration, serration of carapace margin, and in having an elongate and coiled trachea. They differ in a combination of other characters, sufficiently distinct and closely correlated to preclude the possibility that we are dealing with a polymorphic species. In spite of a certain amount of individual variation in single characters, the total differences do hold up in series. *K. homeana* is the rarer of the two, but neither species is well understood biologically and no information is available regarding differences in dietetic or other ecology.

TABLE 7

Characters of the Species of KINIXYS

Kinixys belliana	*Kinixys homeana*	*Kinixys erosa*
Carapace pattern usually radiate, variable	Carapace pattern indistinguishable as between these two species[1]	
Carapace margin neither spinose in young nor serrate in adults	Carapace margin spinose in young and sharply serrate in adults	
Rear end of carapace steeply sloping from *middle* of 5th vertebral	Rear end of carapace overhanging or vertical from *anterior* end of 5th vertebral	Rear end of carapace sloping; if vertical then from *middle* of 5th vertebral
Nuchal scute present, rarely absent	Nuchal scute present, rarely absent	Nuchal scute absent, rarely present
5-9 scutes on forelimb from elbow to outer claw	5-8 scutes on forelimb from elbow to outer claw	3-5 scutes on forelimb from elbow to outer claw
Postorbital bar of skull very thin, elongate, loose or sometimes absent	Postorbital bar of skull moderately thin (thinner and longer than in *erosa*)	Postorbital bar of skull rather short and stout
Habitat in savannas	Habitat in virgin forests	

Key to the Species and Subspecies of KINIXYS

1. Posterior margin of carapace not or but slightly reverted and serrated, never spinose in young; nuchal shield normally present..... 2
   Posterior margin of carapace more or less strongly reverted and strongly serrated, spinose in young; nuchal shield present or absent..... 3
2. Forelimb with 5 claws (though occasional 4-clawed individuals occur throughout much of the range). Range: Madagascar. Eritrea southwest to Natal, northwest through Beehuanaland and Angola to French Cameroon .....*b. belliana Gray* (p. 384)
   Forelimb with 4 claws (all known specimens have 4). Range: Nigeria west to Senegal .....*b. nogueyi* Lataste (p. 396)
3. Nuchal present, rarely absent; posterior portion of carapace from an-

[1] For full description, see p. 408 and Pl. 14 *B, C.*

terior part of the fifth vertebral descending abruptly, either vertically or overhanging. Range: Belgian Congo northwest to French Guinea ..... *homeana* Bell (p. 400)

Nuchal absent, rarely present; posterior portion of carapace descending gradually, if vertical, then from middle of the fifth vertebral. Range: Uganda and Belgian Congo northwest to Gambia..... *erosa* Schweigger (p. 404)

Kinixys belliana belliana Gray

1831c. *Kinixys Belliana* Gray, Synopsis Reptilium, p. 69: No locality ("W. Africa?" was added later by Boulenger, but appears doubtful).
1831b. Gray, 6 (as "*Test.* (*Kinyxis*) *Belliana*").
1835. Duméril and Bibron, 168.
1855. Gray, 13, pl. ii.
1863f. Gray, 196.
1864a. Gray, 169 (reprint of 1863f).
1865. Strauch, 40.
1870e. Gray, 13.
1872c. Gray, 6.
1873b. Gray (part), 16.
1910. Meek, 414.
1919. Schmidt, 406, 600, pl. xi, fig. 2.
1928d. Loveridge, 49.
1929. Flower, 25.
1929h. Loveridge, 14.
1931. Hewitt, 466.
1933. Schmidt, 4.
1934. Pitman, 307.
1936h. Loveridge, 19.
1937a. Flower, 5.
1937f. Loveridge, 495.
1937. Ruckes, 101, pl. x, fig. 8.
1939b. FitzSimons, 18.
1940. Parker, Moreau and Pakenham, 311.
1940a. Scortecci, 126.
1941a. Angel, 151.
1941. Moreau and Pakenham, 109.
1942e. Loveridge, 247.
1943. Scortecci, 270.
1946b. Mertens, 39, 68.
1949. Conant and Hudson, 4.
1950. Rose, 346, figs. 209-210.
1950f. Laurent, R., 133.

1950. Williams, 551.
1951. Monard, 168.
1835. *Cinothorax belliana* Fitzinger, 108.
1843. *Cinixys belliana* Fitzinger, 29.
1849. Smith, A., App., 1.
1854a. Peters, 215.
1866a. Bocage, 40.
1866b. Peters, 887 (*Cinyxis*).
1869a. Peters, 11.
1870. Blanford, 444.
1871b. Sclater, P. L., 544.
1878a. Peters, 202.
1880c. Vaillant, 34, 88.
1882a. Peters, 5.
1886. Vaillant, 137.
1887a. Bocage, 209. (*Cinnixys*).
1887b. Bocage, 86.
1887a. Müller, F., 295 (*Cinyxis*).
1889a. Boulenger, 143.
1890. Strauch (part), 62.
1893a. Boettger, 8.
1893. Trimen, 79.
1894c. Günther, 85 (*Cinyxis*).
1895a. Bocage, 2.
1895. Prato, 19 (*Cynixis*).
1895c. Werner, 127 (*Cininyxis*).
1896a. Bocage, 97.
1896c. Boulenger, 15.
1896. Tornier (part), 2 (*Cinicys*).
1897g. Boulenger, 277.
1897. Tornier, 63.
1898a. Boulenger, 716.
1898. Jeude, 5.
1898. Johnston, 361 (*Cinyxis*).
1898. Sclater, W. L., 96.
1898. Tornier, 282.
1898a. Werner, 203.
1899a. Mocquard, 218 (*Cinyxis*).
1901. Gadow, 365.
1901. Sordelli, 111, figs. 1-2.
1902d. Boulenger, 445 (*Cinyxis*).
1902. Scherer, 253, photo.
1902b. Tornier, 580.

1902e. Tornier, 665.
1905h. Boulenger, 252.
1905. Neumann, 389.
1906b. Siebenrock, 2, 39, fig. 1.
1907a. Boulenger, 6.
1907j. Boulenger, 482, fig. 140.
1907a. Duerden, 9.
1907. Siebenrock, 6.
1908. Chubb, 220.
1908e. Kammerer, 776.
1908b. Mocquard, 557.
1908. Odhner, 2.
1909a. Chubb, 592.
1909b. Chubb, 34.
1909a. Siebenrock (part), 510.
1910. Müller, L., 622.
1910. Roux, 100.
1910. Sternfeld, 4.
1911c. Boulenger, 162.
1912c. Sternfeld, 200.
1912b. Werner, 424.
1913. Boettger, 345.
1913c. Nieden, 54.
1913d. Werner, 40.
1916. Calabresi, 42.
1916. Siebenrock, 6.
1917. Sternfeld, 412.
1919g. Boulenger, 12 (*Cinyxis*).
1919. Siebenrock, 276.
1921d. Loveridge, 50.
1922d. Loveridge, 523.
1922b. Procter, 515.
1923g. Loveridge, 924, 931.
1924b. Loveridge, 2.
1924a. Werner, 266.
1927. Calabresi, 37.
1928. Cott, 952.
1928b. Scortecci, 334.
1929. Rose, 189.
1930a. Scortecci, 215.
1931. Monard, 109 (*Cynixis*).
1933m. Witte, 67.
1937b. Monard, 146.

1954. Noël-Hume, 72.

1845a. *Kinixys schoensis* Rüppell, Mus. Senckenberg, **3**, p. 226, pl. xvi, figs. 1-3: Shoa, southern Ethiopia.

1845b. Rüppell, 297.

1922a. Mertens, 168 (lists type in Mus. Senckenberg).

1847. *Testudo geometrica* Bianconi (not of Linnaeus), 52, pl. vi, figs. 1-2.

1882a. Peters, 3 (corrects Bianconi's misidentification of *belliana*).

1863b. *Kinixys Spekii* Gray, Ann. Mag. Nat. Hist. (3), **12**, p. 381: Central Africa (i.e. probably northwest Tanganyika Territory).

1870c. Gray, 14.

1931. Hewitt, 469.

1935. Hewitt, 347.

1936j. Loveridge, 218.

1937f. Loveridge, 492, 495.

1943. Scortecci, 270, 282.

1890. *Testudo areolata* Strauch (part; not of Thunberg), 58 (Victoria Nyanza specimen only).

1902b. *Homopus darlingi* Boulenger, Proc. Zool. Soc. London, **2**, p. 15, pl. iv: Salisbury District, Mashonaland, Southern Rhodesia.

1906. Duerden, 408, pl. xi, fig. 3.

1907. Duerden, 68, fig.

1920c. *Testudo Loveridgii* Boulenger (part: the small specimen without locality was erroneously attributed to *loveridgii*), p. 264.

1920. *Hinged Land Tortoise* Carpenter, 186 (Lake Victoria).

1927c. *Cinixys lobatsiana* Power, Trans. Roy. Soc. S. Africa, **14**, p. 410, pls. xix-xx: Lobatsi, Bechuanaland Protectorate.

1931. Power, 46, 49, figs. 1-2.

1931. *Kinixys belliana zombensis* Hewitt, Ann. Natal Mus., **6**, p. 469, fig. 1c, pl. xxxviii, fig. 4: Zomba, Nyasaland.

1934a. Mertens and Müller *in* Rust, 8.

1935. Hewitt, pl. xxxiv, fig. 1 (not mentioned in text).

1931. *Kinixys belliana zuluensis* Hewitt, Ann. Natal Mus., **6**, p. 471, figs. 1a-1b, pl. xxxviii, figs. 1-3, 5-10: Richard's Bay, Zululand.

1934a. Mertens and Müller *in* Rust, 8.

1935. Hewitt, 350, pl. xxxv, figs. 1-2.

1931. *Kinixys australis* Hewitt, Ann. Natal Mus., **6**, p. 477, pl. xxxvi, figs. 4-6: White River, eastern Transvaal.

1931. *Kinixys darlingi* Hewitt, 481.

1934a. Mertens and Müller *in* Rust, 8.

1934. Pitman, 307.

1931. *Kinixys jordani* Hewitt, Ann. Natal Mus., **6**, p. 481, pl. xxxvii, figs. 7-9 (not figs. 1-3 as stated): Isoka, Northern Rhodesia.

1934. Pitman, 307.

1931. *Kinixys youngi* Hewitt, Ann. Natal Mus., **6**, p. 486, fig. 1d, pl. xxxvii, figs. 4-5: Shore of Lake Nyasa below Livingstonia, Nyasaland.
1934a. Mertens and Müller *in* Rust, 8.
1949. Moyle, 582.
1931. *Kinixys lobatsiana* Hewitt, 488, figs. 1e-1f and 2, pl. xxxvii, figs. 6-7.
1934a. Mertens and Müller *in* Rust, 8.
1932. *Kinixys australis mababiensis* FitzSimons, Ann. Transvaal Mus., 15, p. 37: Tsotsoroga Pan, Mababe Flats, Bechuanaland Protectorate.
1934a. Mertens and Müller *in* Rust, 8.
1935b. FitzSimons, 302, pl. x, figs. 1-3.
1934a. *Kinixys australis australis* Mertens and Müller *in* Rust, 8.
1934a. *Kinixys belliana belliana* Mertens and Müller *in* Rust, 8.
1937b. Mertens, 5.
1938e. Mertens, 430.
1952. Witte, 12.
1953e. Loveridge, 158.
1953h. Loveridge, 140.
1953. Witte, 15, pl. iv, fig. 1.
1955b. Mertens, 52.
1934a. *Kinixys belliana spekei* Mertens and Müller *in* Rust, 8.
1935. *Kinixys natalensis* Hewitt, Rec. Albany Mus., **4**, p. 353, pl. xxxv, figs. 3-4: Jameson's Drift, Tugela River Valley, Natal.
1937a. *Kinixys zuluensis* Hewitt, 791, fig. 5 (of foot).
1942e. *Malacochersus tornieri* Loveridge (not of Siebenrock), 248 (misdet., juvenile found dead, crushed and dried).
1946. *Kinixys zombensis* Mitchell, 19.

Further citations of *Kinixys*, or *Cinixys, belliana* will be found under *K. b. nogueyi*.

Common names. Bell's Eastern Hinged-Tortoise; *doba* (at Tete:Peters); *enfudu* (Ganda:Carpenter); *fudi* (Pokomo:Loveridge); *furgobi* (Gogo:Loveridge); *furu* (Cewa:Mitchell); *imbati* (at Ngangela:Monard); *kakafula* (eastern Angola:Laurent); *Kamba* (Manganja & Sena:Mitchell); *kobi* (Mwera: Loveridge); *nambi* (Makonde and Mawiha:Loveridge); *ngongo* (Yao:Loveridge; Mitchell); *nguru* (Sagella and Taita:Loveridge); *ufutu* (Matabele:Chubb); *umbeo* (in Benguela:Bocage).

Description. Beak not or but weakly to moderately hooked, uni- or tricuspid; edge of jaws not serrate; prefrontal large, entire, semidivided or divided longitudinally, rarely broken up; frontal large (occasionally divided longitudinally), moderate or broken up; upper head shields small, irregular; forelimb anteri-

orly covered with a few or many, large, unequal, scattered or juxtaposed, strongly imbricate or non-imbricate, more or less pointed (subcircular or pointed in young, subacute in adults) scutes which on anterior edge form a longitudinal series of 5-9 from elbow to outer claw; claws 5, rarely 4 [1]; hinder side of thigh without enlarged tubercles; heel with or without well-defined spurlike tubercles; claws 4, rarely 3 [2]; tail terminating in a more or less distinct horny tubercle that is sometimes much larger in ♂ ♂.

Carapace moderately convex or markedly flattened dorsally, sides sloping, scarely or not (though sometimes deeply [3]) notched

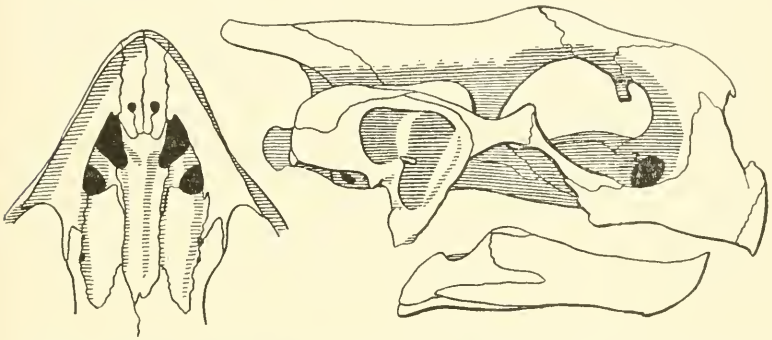


Fig. 46. Skull of *Kinixys b. belliana* (A.M.N.H. 10029). Condylobasal length 37 mm.

(S. McDowell del.)

in nuchal region; anterior margin not or but slightly expanded, not or but slightly reverted, not spinose in young, posterior margin not expanded, not or but slightly reverted, not or but slightly (occasionally moderately[4]) serrated, not spinose in young, rear

[1] Four in 2 out of 23 tortoises from Uele region of Congo, a third had 4 on one forefoot and 5 on the other (Schmidt:1919:407); four in 3 (M.C.Z. 40011, 40013, 40017) out of 8 Kenya specimens, and four on both forefeet of 1 (M.C.Z. 44451) of 8 Southern Rhodesia tortoises examined by us. This Rhodesian tortoise is unusual in that it is the fourth claw that is lacking; four in a juvenile only of a series of at least 6 from Beira (Boulenger: 1907): 482 and Hewitt: 1935: 353). The missing claw on each forefoot is represented by a light-colored, rounded tubercle (Battersby in letter of 15.xii.54). All 14 Tanganyika and all 24 Nyasaland specimens in the M.C.Z. have the normal five claws of *b. belliana*.

[2] Three in a Belgian Congo tortoise mentioned by Schmidt (1919: 407).

[3] Deeply notched in an Mtimbuka juvenile (M.C.Z. 50328) as the nuchal is absent.

[4] Moderately serrated in type of *lobatsiana* Power (1927c:pls. xix-xx).

end in young sloping more or less steeply, in adults even more so; dorsal shields concentrically striated, the striations more or less reduced by wear in aged specimens, not or only sometimes swollen,[1] not convex; nuchal usually elongate, though as broad as, or much broader than, long in very young, occasionally divided, minute[2] or absent;[3] vertebrals 5, rarely 4,[4] 6 or 7,[5] not or but slightly convex, first broader than long in young, broader than long, as broad as long, or longer than broad in adults; second to fifth as broad as, or broader than, long; second broader, subequal to, or narrower than, fifth in young, narrower in adults; fifth flat in young, more or less convex in adults; costals 4, rarely 3[6] or 5,[7] usually not forming an angle with the marginals; marginals 9-12,[8] usually 11; supracaudal undivided, rarely divided,[9] with or without a tendency to be incurved in ♂ ♂, otherwise not or but slightly reverted in both sexes.

Front lobe of plastron anteriorly truncate, very thick, not or but slightly or moderately projecting beyond the anterior border of the carapace, not bifid, not or very openly notched; gulars paired; pectorals[10] moderate, their anterior borders straight or widening more or less gradually towards the axillary notch; axillaries 2-4, the innermost small, inconspicuous or absent, the outermost more or less concealed; inguinal 1,[11] large, in contact

1 Strongly swollen, with deep gutters between the shields, in 3 Mafia Island tortoises (*fide* Siebenrock: 1906b: 2).

2 Divided in a juvenile (U.S.N.M. 41699). When rudimentary it may result in the marginals meeting either before or behind it (Strauch: 1890).

3 Absent in an Mtimbuka juvenile (M.C.Z. 50328) and in one of a Beira series (Hewitt: 1931).

4 Four in a carapace from Moroni figured by Sordelli (1901:111) with consequent elongation of the third vertebral, etc.

5 Six or seven in an Ujiji and some Mtimbuka adults (M.C.Z. 48001; 50318; 50323).

6 Three on right side of a Garamba ♀ (A.M.N.H. 10047) where the missing costal is replaced by an extended vertebral that is in contact with the marginals.

7 Five in an Mtimbuka ♂ (M.C.Z. 50318).

8 Nine on left, ten on right of Moroni carapace (Sordelli:1901); ten on right, eleven on left in a Sandown ♀ (Hewitt); twelve on left side of an Ithanga juvenile (M.C.Z. 8158(and twelve in an Mtimbuka ♀ (M.C.Z. 50323) with the hinge between marginals 8 and 9 instead of between 7 and 8, the normal arrangement; twelve in an Ujiji ♂ (M.C.Z. 48001) whose hinge is between marginals 7 and 8; in an Angolan tortoise the hinge was between 6 and 7 (*fide* Bocage: 1866a), as also in a Natal specimen mentioned by Hewitt (1935).

9 Divided in a Mussera tortoise (*fide* P. L. Sclater:1871b); also in several from Natal, made cotypes of *natalensis* (Hewitt: 1935).

10 Pectoral on right side of a Cheren ♂ is fused with the corresponding abdominal shield (Scortecci: 1928b); pectorals fail to meet in an Uele tortoise (A.M.N.H. 10031) mentioned by Schmidt (1919: 407).

11 Absent in a Natal tortoise (*fide* Hewitt:1935:353).

with the femoral; hind lobe very short, truncate, not or but slightly notched posteriorly.

Plastral formula: Abh>, h>(g, p, f, an, all extremely variable).

Color. Carapace straw-colored, yellowish brown, olivaceous brown or reddish brown; in young uniform, or the areolae deep brown surrounded by a zone of yellow which may extend to the margins of each shield or be interrupted by fine black radiations from the darker areolae or be entirely replaced by black edging. The juvenile coloring may persist in adults, though usually with the modification that the black edging of the shields is irregularly or symmetrically broken up by yellow pigment, or only the black areolae of the juvenile pattern persists, in which event it is frequently interrupted by a median, longitudinal, yellow streak. In a few individuals, chiefly ♂ ♂, the coloring may be uniform.

Plastron horn color, uniform or smudged with black, the latter sometimes in the form of radiations from around the areolae.

The literature teems with descriptions of deviations of the above, for the coloring of *belliana* is extremely variable — due in part to the normal zonary pattern of the young being replaced by the secondary or radiate arrangement found in adults, in part because ♂ ♂ tend towards uniformity while ♀ ♀ are apt to be darker.

Size. Carapace length of largest ♂ (M.C.Z. 18151) from Turiani, 193 mm., breadth 125 mm., height 83 mm.; carapace length of largest ♀ (M.C.Z. 50321) from Mtimbuka, 207 mm., breadth 135 mm., height 88 mm. Possibly the smallest, from Uliya, length 50 mm., breadth 46 mm., height 25 mm. (All three collected by Loveridge.)

That the *belliana* of open savanna have higher shells, while the more depressed *spekii* type live in rocky terrain, where they may seek shelter beneath boulders, was suggested by Loveridge (1923g:924) who, both then and later (1936j:1942e:1953e), furnished tabulated measurements. In 1942 he reluctantly returned *spekii* to the synonymy in the absence of evidence that the low-vaulted form, which predominates in certain localities like Mtimbuka, has any zoogeographical significance. With this decision we concur after careful reappraisal of all available material and data.

Sexual dimorphism. In addition to a certain amount of sexual dichromatism among adult *belliana,* as indicated above, the most promising aids to determining sex are:

Plastron usually somewhat concave along the median axis; anal shields forming an almost straight edge posteriorly; tail very long, normally terminating in a large horny tubercle ..... ♂

Plastron flat; anal shields forming an incurved edge posteriorly; tail short, normally terminating in a very small horny tubercle ..... ♀

The caudal tubercle is not always so well-developed in males as to be the infallible guide to sex supposed by Sternfeld (1917: 412).

Breeding. On October 10, at Lumbo, a 207 mm. ♀ held a mass of ovules ranging from pea-sized to 28 mm. in diameter; of the latter there were about 15 (Loveridge:1921d).

In May, 2 oval eggs were present in one tortoise, and 3 each in two other Mafia Island ♀ ♀ (Siebenrock:1906b:fig. 1), their dimensions correlated with those of the parent, for the eggs of a 168 mm. tortoise measured 41 x 33 mm., those of a 192 mm. reptile 45 x 36 mm.

Longevity. Nine years and 9 months (Conant and Hudson: 1949); 9 years, 3 months, 28 days (Flower:1937a).

Diet. Frequently seen feeding on fallen bananas and mangoes; two were observed eating sugar cane in a plantation during a downpour (Scherer:1902). Four found feeding on fungi at Lobatsi (Power:1927c); fungi (Mitchell:1946); take pawpaw readily (Loveridge:1928). Though plenty of grass was present in the enclosure, Loveridge (1923g:925) found one of these tortoises eating hard Indian corn; a single kernel would be taken up and dropped five or six times before being swallowed. Another *Kinixys,* munching something at the time, was found nosing a large yellow carpenter bee (*Xylocopa nigrita*) of whose hind legs one was missing. Though the tortoise was seen to return again and again to the bee, it never actually bit it. The insect, which had only recently died, had probably fallen from a beam above. A ♂, feeding in bright sunshine beside the Voi road, made off with surprising agility when approached (Loveridge:1936j: 220).

Parasites. Ticks (*Amblyomma nuttalli*)[1] have been recorded from many localities (Loveridge). Nematodes are commonly found in the intestines of Congo tortoises (Lang, *in* Schmidt: 1919).

Enemies. In Angola the natives esteem these tortoises as food (Anchieta, *in* Bocage:1895a). In Faradje district of the Belgian Congo, following the grass fires of February and March, the Azande and Logo organize tortoise-hunts. The reptiles are located by the natives' dogs, and the animals unearthed by the iron-shod butts of spears. The rear portion of the carapace is readily separated at the hinge and the meat removed for stewing. The stomach and cloaca are usually rejected but the rest of the reptile, including nematodes which are thought to add to the flavor, are dropped in the cooking pot. These tribesmen of the northeast Congo apparently prefer tortoises to chicken, and fancy them more than the semi-aquatic terrapin (Pelomedusidae) which have a strong musky odor (Lang, *in* Schmidt:1919:410).

Apart from man, *Kinixys* appears to have few enemies. However, Lang records finding the shell of a recently eaten one whose carapace and plastron were marked by the teeth of a leopard the tracks of which were plainly visible. In East Africa tortoises may sometimes be found wandering about with shells that have been bitten by hyenas or other carnivores, the scars completely healed. The empty shell of one specimen (M.C.Z. 18153) is studded with tooth marks and the bone re-ossified where an extensive piece has been broken right off.

A *Kinixys* with carapace fractured and bleeding, as if dropped from a height by some bird of prey, was found by Carpenter (1920:186).

Defense. When picked up, a Bell's Box-Tortoise may snap its beak and struggle wildly, so that its captor is liable to be scratched by the flailing forelimbs or wet by the pungent cloacal fluid that is discharged. Another individual may emit a hiss as it withdraws its head within the sheltering carapace, completing its concealment by bringing forward and folding the heavily armored forelimbs. Simultaneously, air is expelled from the lungs as the rear portion of the carapace comes down to enclose the hind limbs and tail (Lang, *in* Schmidt:1919).

[1] Early records of *A. marmoreum* were based on ticks that have been re-examined by Dr. J. C. Bequaert and found to be *nuttalli*.

Aestivation. At the commencement of the dry season (December to May) in the Uele, by burrowing among the roots of trees, into termitaria, or a few inches below ground, *Kinixys* usually escapes the devastating grassfires, remaining quiescent until aroused by the onset of the rains (Lang, *in* Schmidt:1919:410).

Habits. In the coastal belt of the Congo, where it inhabits low granite hills, *Kinixys* appears only in the hot rainy season (October to May) remaining underground during the cold weather according to the natives (Sclater:1871b:544). Fairly common in the savanna of the northeast Uele where they find shelter and food in the dense undergrowth of the moister areas bordering swamps and shallow watercourses. During the rainy season they wander further afield so that the natives have difficulty in locating them in their dry-season haunts. At the beginning of the rains (June) three of the tortoises were found in a shallow pool, overgrown with vegetation. One, released near a river, walked to the edge of the steep bank and unhesitatingly dropped into the water where, though powerless against the strong current, it appeared at ease (Lang, *loc. cit.*). Found beneath bushes and in thickets along the river banks of Eritrea (Blanford:1870). In Tanganyika commonly encountered during the rainy season in damp areas of the savanna (*fide* Böhm), also in a papyrus swamp according to Stuhlmann (Tornier:1896). Plentiful at Broken Hill during rains (Pitman:1934). J. M. McCallum (*in* Hewitt: 1935:494) reports on the readiness with which "*lobatsiana*" will enter water. A 75 mm. juvenile was found in a termitarium at Entendweni, Zululand (Odlmer:1908).

Though members of this genus are said to usually walk on the claws of their forefeet, *lobatsiana* places "the palms on the ground at every step and can remain standing on the palms, the carapace being raised a little from the ground" *fide* Hewitt (1931:500;footnote).

In captivity these tortoises thrive best when kept under humid conditions at high temperatures *fide* Kammerer (1908b:770). Instead of taking advantage of the shelters provided for them at Kilosa, seven *K. b. belliana* were apt to stay out at night, particularly when raining, spending the entire night in efforts to escape from their enclosure (Loveridge *in* Procter:1922b:523, where its habits are contrasted with those of *Malacochersus*).

Localities. Sudan: Khartoum; Liranga; Moroni; Talodi, Nuba Mountain Province; Sudan (as "Sandom"[1]); *Torit. *Eritrea:* Anseba Valley; Asmara; Cheren. *Ethiopia:* El Direre, Tertale; Errer (Erer) River near Harar; Shoa (Schoa). *British Somaliland:* Berbera. *Somalia:* "Adden Cabola"[2] (? Caboba); "Badditu to Dime"; Webi River in Ennia-Gallaland. *Uganda:* Busu Hill; Busu (Bussu) near Jinja; Masindi; Mount Elgon. *Kenya Colony:* Athi Plains; *Golbanti; *Ithanga Hills; *Kibwezi; Kitui; Moyale; Mtito Andei; Nairobi; Taru; Tereale (Pozzi-); *Voi; Yatta Plains. *Tanganyika Territory:* Amboni near Tanga; Bubu near Kondoa; Bukome; "Central Africa" (for type of *spekii*); Dodoma; Godegode; Ikikuyu; Kakoma; Korogwe (Kerogwe); Kigoma; Kilimanjaro Mtn.; *Kilosa; *Kiponda to Mitungu; Kiserawe; *Kitaya; Kongonda near Dodoma; Lake Rutamba; Lake Tanganyika; Lake Victoria; Longido West; Mafia Id.; Maji ya Chumvi; Mbulu near Arusha; *Mikindani; Mkata River; Mkomasi River; Morogoro; Mugango. 24 km. S. W. Musoma; Myombo; *Nchingidi, Rondo Plateau; Ngoga; Nyangesi, Usukuma; Pangani River bank; Pwaga; *Simbo near Tabora; Tamborale (Muana Tomboloo); Tanga; *Turiani; *Ujiji; Uliya. *Zanzibar Island:* Mafia Id.; *Zanzibar (Müller: 1887a; Strauch: 1890; etc.). *Mozambique:* Amatongas; Beira; Boror; Caia; Charre; Chitau; Gauca; Inhambane; Lumbo; Mesuril; Sena; Tete. *Nyasaland:* Angoniland; Chibotela; Chikwawa; Chiromo; Chitala River; *Cholo Mtn.; Fort Johnston; Lake Shirwa (Chilwa); Lakeshore below Livingstonia; Likangala; Monkey Bay; *Mpimbi near Zomba; *Mtimbuka; Port Herald; Zomba. *Northern Rhodesia:* Broken Hill; *Isoka; Petauke. *Southern Rhodesia:* *Birchenough Bridge; *Bulawayo; Changadzi River; Essevale; *Hot Springs; Marandellas to Umtali; Mazoe; Salisbury district; Sandown; *Selinda Mtn. and valley at its foot; Shangani River. *Bechuanaland Protectorate:* Lobatsi; Tsotsoroga Pan, Mababe Flats. *Transvaal:* Glentig near Nylstrom; Naauwpoort; White River. *Natal:* Dimani's Stream; Entondweni (Entendweni); Impanza near Greytown; Jameson's Drift; Manaba; Matubatuba; Natambana; Richard's Bay; Tugela River and Valley; Umfolosi Station. *Angola:* Caconda;

[1] In Boulenger (1889a), correction confirmed by J. C. Battersby (15.xii.1954).

[2] In Calabresi (1916), reporting on the Stefani and Paoli material with many misspellings.

Capangombe; Caquindo (Kakindo); Chitau (C.M.) Cubal; Cubango (Kuvangu); Duque de Bragança; Ebanga; Galanga; Gauca (C.M.) Lui River, Muata-Yamvo region; Lunda; Mbale River; Muita; Osi; Quissange; Vila da Ponte. *Belgian Congo:* Abimva; Avakubi; Bowa River; Cape Tembwe; Dika; Faradje; Ganza; Garamba; Kabambaie; Kabulumba; Kansenia; "Kanzluze"; *Kapiri; Kasonga to Uvira; Kaswabilenga; Kateke; *Lukafu; Lukonzolwa; Mahagi Port; Manda; Masombwe; Mpala; Mulungwe River; Musosa; Musserra; Niangara; Northwest shore of Lake Tanganyika; Uele region. *French Cameroon:* Meiganga; Yoko (5 claws present on forefeet of both).

Madagascar: Ambanja (two alive: Angel:1941a:151); Ambassuara (Peters:1873c:792); Nosy (Nossi) Bé (Boettger:1889: 295).

Range. Eritrea southwest to Natal, northwest through Bechuanaland and Angola to French Cameroon where it meets with the western race. Also Madagascar. (The possibility of its having been introduced here should not be overlooked. But for Angel's recent record from northern Madagascar, we might have questioned its occurrence, half a century having elapsed since the indefinite records of Müller, Strauch and others.)

Kinixys belliana nogueyi (Lataste)

1844. *Kinixys belliana* Gray, part, not of Gray 1831, p. 12.
1855. Gray (part), 13, pl. ii.
1873b. Gray (part), 16.
1884a. Rochebrune, 16.
1857. *Cinixys Belliana* Jan (not of Gray 1831), 35.
1890. Strauch (part), 62.
1893c. Matschie, 208.
1896a. Bocage, 74.
1901c. Tornier, 66.
1906i. Boulenger, 197 (as *Cinyxis*).
1906b. Siebenrock, 3.
1907j. Boulenger, 482.
1907. Siebenrock, 6.
1909. Gendre, cvi.
1921a. Chabanaud, 461.
1921b. Chabanaud, 522.
1937. Andersson, 3.

1886. *Homopus Nogueyi* Lataste, Le Naturaliste (2), **8**, p. 286: Medina (as Médine), Upper Senegal.
1889a. Boulenger, 148.
1901c. Tornier, 67.
1906c. Duerden, 408.
1888a. *Cinixys Dorri* Lataste, Le Naturaliste (2), **10**, pp. 164, 226, fig. 1: Bakel, Upper Senegal.
1903b. *Cinixys nogueyi* Siebenrock, 185, 442.
1931. *Kinixys nogueyi* Hewitt, 468.
1934a. *Kinixys belliana nogueyi* Mertens and Müller *in* Rust, 8.
1952a. Loveridge, 231.
1955. Cansdale, 89, 103.

Common names. Bell's Western Hinged-Tortoise. *Nkounou* (in Senegal: Roehebrune).

History. The species was named for M. Gustave Noguey of the Linnaean Society of Bordeaux. Siebenrock (1903b) was the first to detect Lataste's error in assigning *nogueyi* to the genus *Homopus;* he also re-examined the eleven Togo tortoises referred to *belliana* by Tornier (1901e) and found that all had 4 claws on the forelimbs. Boulenger (1906i) questioned Siebenrock's action in making *nogueyi* a full species, pointing out that in some West African examples radiating black streaks *are* present, while the gular/anal proportions do not differentiate *nogueyi* from *belliana.* Boulenger regarded *nogueyi* as a 4-clawed variety of *belliana.* Later (1907j) he reported a young *belliana* from Beira, Mozambique, as having only 4 claws (though the adults from the same locality had 5), so concluded that *nogueyi* was inseparable. Loveridge (1952a), after studying five 4-clawed tortoises from Togo and Dahomey, regarded it as a West African race and defined the range.

Description. Beak weakly to moderately hooked, uni- or bicuspid, edge of jaws not serrate; prefrontal divided longitudinally; frontal large or small, occasionally divided longitudinally; upper head shields small, irregular; forelimb anteriorly covered with a few, large, unequal, scattered or juxtaposed, strongly imbricate, subcircular or subacute scutes which on the anterior edge form a longitudinal series of 6-7 from elbow to outer claw; claws 4; hinder side of thigh without enlarged tubercles; heel without, or with a trace of an enlarged tubercle; claws 4.

Carapace moderately convex, flattened dorsally, sides sloping in young, descending abruptly in adult, not or but openly notched in nuchal region; anterior margin somewhat expanded and not or but slightly reverted, not serrated, not spinose in young; posterior margin not expanded, not or but slightly reverted, not serrated, not spinose in young; rear end in young sloping gradually, in adults vertically from the middle of the fifth vertebral; dorsal shields concentrically striated (the striations more or less reduced by wear in aged specimens), neither swollen nor convex.

Nuchal about as long as broad in young, elongate in adults; vertebrals 5,[1] without median keel (except in young which may show the barest trace), not convex, first broader than long in young, longer than broad in adults, second to fifth broader than long, second as broad as fifth in young, narrower in adults, fifth flat in hatchlings, somewhat convex in adults; costals 4, not forming an angle with the marginals; marginals 11-12 [2]; supracaudal undivided, more or less reverted; tail terminating in a horny tubercle.

Front lobe of plastron very thick, not or but slightly projecting beyond the anterior border of the carapace, not or but scarcely notched; gulars paired; pectorals moderate, their anterior border widening gradually towards the axillary notch; axillaries 3, the innermost small, the outermost more or less concealed; inguinal large, in contact with the femoral; hind lobe very short, truncate, not notched posteriorly.

Plastral formula: Abd>h>g>or=or<f>p>or<an.

Color. Carapace light olive green or reddish brown, uniform, or each dorsal shield with yellowish green areolae and bordered with black, which may be interrupted at the angles. Plastron yellow, or greenish yellow, more or less marked by black or reddish brown.

Size. Carapace length of a ♂ (I.F.A.N. 2052) from Bassila, 148 mm., carapace length of largest Togo tortoise, unsexed, in Berlin Museum, 220 mm.; largest ♀ (I.F.A.N. 2052 also) from Bassila, 152 mm.; of the type ♀ (B. M.) from Medina, 135 mm., breadth 99 mm., height 60 mm. Carapace length of a juv. (M.C.Z. 51755) from Tohoun, 48 mm.

[1] A relatively small azygous shield split off from left side of fifth vertebral in a Kabala ♂ (M.C.Z. 54118).

[2] Twelve on left side only of Kabala ♂ (M.C.Z. 54118).

Diet. Lataste, finding much debris of Coleoptera as well as vegetable matter in the intestines of the ♀ cotype, cites this as evidence of the reptile being insectivorous as well as vegetarian.

Enemies. Ornaments are made from the emptied shell (Cansdale:1955). Loveridge (1952a), noting that the claws and soles of each foot of a Tohoun tortoise appear to have been sliced off with a sharp knife, suggests it may have been done by an African who was afraid of being scratched.

Aestivation. Burrows into the ground during the dry season according to native reports (Cansdale:1955).

Localities. French Cameroon: Garoua (Garua); Konn; Mandara (as Mandana) Highlands (shell only, so race questionable); Mayo Sala; Ndikinimeki; Ngaouyanga; Sajdje (Sakdje); Tibati.[1] *Nigeria:* Gando (Gandu); "Gao Haussari am Garua-Benue"[2]; Lagos. *Dahomey:* *Bassila; Porto Novo.[3] *Togo:* Adele (as Bismarckburg); Lome; Misahöhe (see Höhe); Tohoun (or Tohou). *Gold Coast:* Kintampo; Somanya, Krobo (M.C. Lesage). *Sierra Leone:* *Kabala, Koinadugu district; Musaia.[4] *French Guinea:* Beyla; Forecariah; Kankan; Labe, Fouta-Djalon. *Portuguese Guinea:* Bolama. *Gambia:* MacCarthy Island. *French Sudan:* Diafarabe; Pama, Gourma district (as Pama-Gurma in Tornier:1901c). *Senegal:* Bakel; Kaolack; Medina; Sindia, 50 km. from Dakar (A. Villiers).

Range. French Cameroon west to Senegal.

[1] We are indebted to Dr. V. Aellen and Mons. W. Lanz for examining the specimens from six of these localities in French Cameroon and ascertaining that the forefeet bore 4 claws in every one of the eight tortoises involved.

[2] Apparently this refers to some Gao in the Haussa country of northern Nigeria west of Garoua on the Benue River in French Cameroon, in an effort to distinguish it from the well known Gao on the Niger River. Passare was the collector, states Tornier (1901c: 67).

[3] Specimens from Porto Novo; Lome; Forecariah; Kankan; Diafarabe and Kaolack, all have forefeet bearing 4 claws, writes A. Villiers (11.ii.55, etc.) in whose care they are at I.F.A.N., Dakar, Senegal.

[4] A limbless 58 mm. shell, originally said to have measured 64 mm., so shrinkage during drying may account for the surprisingly abrupt, *homeana*-like declivity of the carapace posteriorly. Collected in northern Sierra Leone in 1948 by T. S. Jones. Now in the British Museum and seen by us.

Kinixys homeana Bell

1827. *Kinixys Homeana* Bell, Trans. Linn. Soc. London, **15**, p. 400, pl. xvii, fig. 2: West Africa (The statement that the types came from Sierra Leone, was later amended by Boulenger (1889a: 143) to Cape Coast, Ashanti, i.e. Gold Coast. Both Bell and Boulenger give Lt. M. C. Friend as the collector.)
1831b. Gray, 6.
1831c. Gray, 15.
1835. Duméril and Bibron, 161, pl. xiv, figs. 2-2a.
1844. Gray, 11.
1845. Wyman, 38.
1850. Berthold, 423, pls. xliii-xlv.
1855. Gray, 13.
1863f. Gray, 170 (reprint of 1863f).
1864a. Gray, 197.
1865. Strauch, 38.
1870e. Gray, 14.
1873b. Gray, 17.
1884a. Rochebrune, 17.
1919. Schmidt, 403, 598.
1929. Flower, 25.
1930a. Barbour and Loveridge, 770.
1934a. Mertens and Müller *in* Rust, 8.
1937c. Loveridge, 269.
1937. Ruckes, 101.
1938b. Mertens, 33.
1941e. Loveridge, 115.
1950. Williams, 551.
1951. Monard, 168.
1955. Cansdale, 89, 103, fig. H5.
1856a. *Cinixys Homeana* Duméril, 372.
1860. Duméril, 162.
1875a. Peters, 196.
1887a. Müller, F., 295.
1889a. Boulenger, 143.
1890. Strauch, 61.
1893c. Matschie, 208.
1897. Sjöstedt, 6.
1898a. Werner, 203.
1899. Siebenrock, 566, pl. i, figs. 1-2.
1900b. Boulenger, 447.
1901. Gadow, 364.
1901b. Tornier, 61.

1902c. Tornier, 665.
1906a. Mocquard, 479.
1909a. Siebenrock, 510.
1910. Müller, L., 622.
1910. Sternfeld, 5, fig. 7.
1911. Lampe, 145.
1911a. Masi, 35.
1912c. Sternfeld, 200.
1916. Siebenrock, 5.
1917. Sternfeld, 412.
1919. Siebenrock, 276.
1921a. Chabanaud, 461.
1921b. Chabanaud, 522.
1954. Noël-Hume, 74.

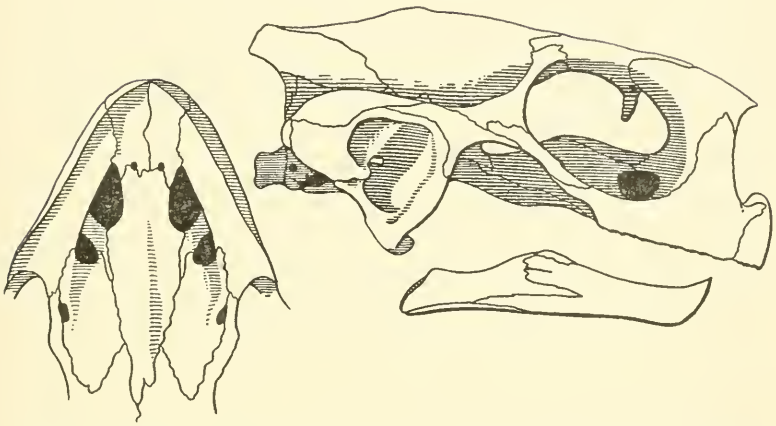


Fig. 47. Skull of *Kinixys homeana* (A.M.N.H. 43306). Condylobasal length 41 mm.

(S. McDowell del.)

Common name. Home's Hinged-Tortoise (Gray).

Illustrations. Bell's (1827) finely executed drawing consists of a lateral view of the shell in black and white to show its abruptly descending rear end in striking contrast to that of *erosa* (as *castanea*) on the same plate. Duméril and Bibron (1835) furnish a colored figure (also lateral), together with a line drawing of the plastral scutes.

Description. Beak moderately to strongly hooked, unicuspid;

edge of jaws not dentate; prefrontal divided longitudinally; frontal large, small, or broken up; upper head shields small, irregular; forelimb anteriorly covered with a few scattered, large, unequal, strongly imbricate, more or less pointed scutes which on the anterior edge form a longitudinal series of 5 to 8 from elbow to outer claw; claws 5; hinder side of thigh without enlarged tubercles; heel with or without a spurlike tubercle; claws 4; tail terminating in a small, somewhat clawlike tubercle that is larger in ♂♂.

Carapace flattened dorsally, sides sloping, not or but openly notched in nuchal region, anterior margin strongly expanded and not or but slightly reverted, spinose in young, posterior margin not expanded, more or less strongly reverted and strongly serrated, spinose in young, rear end in young sloping gradually, in adults vertically from the anterior part of the fifth vertebral; dorsal shields concentrically striated though sometimes scarcely distinguishable, through wear, in aged specimens, neither swollen nor convex (except the fifth vertebral); nuchal elongate, very rarely absent[1]; vertebrals 5, with a slight median keel, first broader than long in young, as long as, or longer than, broad in adults, second to fifth broader than long, the third broader than the third costal; costals 4, rarely 5[2] or 7,[3] not or but rarely forming an angle with the marginals; marginals 11, rarely 12,[3] the anterior much longer than the posterior ones; supracaudal undivided, rarely divided,[4] more or less strongly reverted in both sexes.

Front lobe of plastron very thick, not or but slightly projecting beyond the anterior border of the carapace, openly notched; gulars paired; axillaries 2-4, the innermost, if present, small, the outermost more or less concealed; inguinal large, in contact with the femoral; hind lobe very short, rounded, truncate, notched posteriorly.

Plastral formula: Abd>h>(g, p, f, an, very variable), f or an shortest.

[1] Absent in one Zorzor tortoise (U.S.N.M. 109698) confirming Loveridge (1941e: 115), and in an Oda specimen (C.N.H.M. 53630) studied by E. E. Williams.

[2] Five on left side only of a Nkolembembe tortoise (Sternfeld: 1917).

[3] Five on right, 7 on left, of a Zorzor specimen (U.S.N.M. 109698) which has 12 marginals on left side only (Loveridge: 1941e).

[4] Divided in a juvenile from Gabon (Duméril: 1860).

Color. Essentially similar to that of *K. erosa,* which see.

Size. Carapace length of largest ♂ (U.S.N.M. 10962), from Zorzor, 200 mm., *not* exceeded by a Mujuka ♂ (S.M. 156) of 210 mm. mentioned by Mertens (1938b:33) as it was apparently measured over the curve. Carapace length of largest ♀ (U.S. N.M. 109685), also from Zorzor, 210 mm. (*fide* Loveridge:1941e: 115). The holotype was said to be 190 mm. long, 132 mm. broad, and 85 mm. in height.

Sexual dimorphism. As in *erosa.* The length of the gular suture in relation to the length of the plastron, was found by Loveridge (1941e:115) to have some significance in seven tortoises from Zorzor. It might not hold good for larger series.

Localities. Belgian Congo: Mawambi (Mavambi); northwest of Lake Tanganyika (Siebenrock:1916); near Saidi's Village (Loveridge:1937e). *French Equatorial Africa:* Freneh Congo. *Rio Muni:* Yenghe (Jengwe, Cameroon). *French Cameroon:* Bipindi; Dehane; Dibongo near Edea; Kribi; Nkolembembe (Nkoubembe); Nkoolong (C.M.); *Sakbayeme. *British Cameroon:* Bibundi; Bonge, Meme River; Isongo; Johann Albrechtshöhe; Likomba; Mapanja; Mosake; Mujuka; Victoria. *Nigeria:* Bonny (Boni); *Ifon, Ondo district (M.C.Z.). *Gold Coast:* Abetifi; Ada (C.N.H.M.); Ashanti; Cape Coast Castle. *Ivory Coast:* Adiopodoume (V. Aellen); *Liberia:* *Cape Palmas; *Lenga, Farmington River; Zorzor.

Range. Belgian Congo northwest to French Guinea, or at least Liberia.

Wyman (1845:38) received a shell from the Cape Verde Islands, presumably a human importation. Senegal and Gambia (Rochebrune:1884a) are similarly rejected pending confirmation. The Mawambi record (Sternfeld:1912e), being based on a head and limbs, was questioned by Sehmidt (1919:403). However, later records from the Belgian Congo (Siebenrock:1916; Loveridge:1937c) validate the presence of *homeana* in this general region, so we have tentatively allowed the Mawambi record to stand.

We emphatically reject the alleged occurrence at Kiu, Ukamba, Kenya Colony of such a rain-forest species as *homeana.* Siebenrock (1916:5) evidently entertained doubts for he made enquiries of Lampe respecting it and was assured that the specimen in

question had been presented to the Wiesbaden Museum by a missionary who had personally picked it up at Kiu about 1912. Dr. F. Neubar, Director of Wiesbaden Museum, informs us (7.i.55) that no reference to such a specimen can be found in their catalogue, and also that much of their material was lost in a fire.

In the absence of the specimen, speculation seems idle for many alternative explanations are possible. The simplest is to assume a transposition of specimens in the museum; such things have been known to occur! Again there may have been a mistake as to the provenance of that particular specimen on the part of the collector, who may have previously been stationed at some mission in West Africa. It might be pointed out that in 1912 there were no dining cars on the trains plying between Lake Victoria and Mombasa, so that it was customary to disembark all passengers at Kiu (alt. 4861 feet) for meals at the station restaurant. Thus the possibility of the young tortoise having escaped from the custody of some passenger, homeward bound from the eastern Congo, should not be overlooked.

K. homeana does occur in the extreme eastern Congo; *erosa,* continues eastward, though sparsely, in Uganda. The two agree in the serrated nature of the posterior edge of their carapaces so it is barely possible that Siebenrock might have confused them, though this is unlikely as he (*loc. cit.*) cites the differing scutellation of their respective forearms — 4 or 5 for *erosa,* 5 to 8 in the case of *homeana.* In this respect *homeana* approaches *belliana,* which has 5 to 9 scales on the forearm, and *belliana* is a relatively common reptile in Ukamba. A misidentification with *belliana* would be likely only if the carapace of the Kiu juvenile seemed abnormally serrate to Siebenrock.

K. homeana has been erroneously recorded as occurring in Guadeloupe and Demara, South America, by Gray (1831c), followed by Duméril and Bibron (1835).

Kinixys erosa (Schweigger)

1802. *Testudo Denticulata* Shaw (not of Linnaeus), **3,** p. 59, pl. xiii.

1812. *Testudo erosa* Schweigger, Königsberger Arch. Naturwiss. Math., 1, p. 321: "America septentrionali (Shaw)."

1814. Schweigger, 52 (reprint of 1812).
1826. *Testudo Schöpfii* Fitzinger, Neue Classif, Rept., p. 44: No locality (*nom. nov.*).
1836. Fitzinger, 121.
1827. *Kinixys castanea* Bell, Trans. Linn. Soc. London, **15**: p. 398, pl. xvii, fig. 1: Africa.
1831c. *Kinixys*[1] *erosa* Gray, 16.
1835. Duméril and Bibron, 165.
1844. Gray, 12.
1851. Duméril and Duméril, 6.
1855. Gray, 13.
1856a. Duméril, 372.
1857. Jan, 35.
1859. Cope, 294.
1860. Duméril, 162.
1862a. Strauch, 24.
1863f. Gray, 197.
1864a. Gray, 170 (reprint of 1863f).
1865. Strauch, 39.
1866a. Bocage, 40.
1870e. Gray, 14.
1873b. Gray, 17.
1873h. Gray, 320, pl. xii, fig. 2.
1874. Reichenow, 298.
1875a. Peters, 196.
1877e. Peters, 611.
1880e. Vaillant, 34, 88.
1882a. Müller, F., 165.
1882. Pechuël-Loesche, 278.
1884a. Rochebrune, 17 (ignored).
1884b. Sauvage, 200.
1886. Vaillant, 137.
1887a. Müller, F., 295.
1888a. Boettger, 12.
1889a. Boulenger, 141, figs. 40-41.
1890. Büttikofer, 436, 478.
1890. Strauch, 61.
1893a. Boettger, 8.
1893c. Matschie, 208.
1895a. Bocage, 1.
1895e. Werner, 127 (*Cininyxis*).
1897. Sjöstedt, 6.

[1] Variously misspelled *Kinyxis, Cinyxis* and *Cinixys* in a few of the citations following.

1898. Jeude, 5.
1898a. Werner, 203.
1900. Boulenger, 447.
1901. Gadow, 364, fig. 82.
1902c. Tornier, 664.
1905. Barbier, 84, pl. iii.
1905f. Boulenger, 183.
1906i. Boulenger, 197.
1906. Johnston, 820, 833.
1906a. Mocquard, 479.
1907. Johnson, 11, 68, photo.
1907. Siebenrock, 2, fig. —, pl. i.
1908c. Kammerer, 775, fig. 15.
1909a. Siebenrock, 509.
1910. Sternfeld, 4, fig. 6.
1911. Lampe, 145.
1912b. Werner, 424, fig.
1916. Siebenrock, 4, figs. 1-2.
1917. Sternfeld, 408, 411.
1919g. Boulenger, 11.
1919. Schmidt, 403, 598, pl. xi, fig. 1, map 3.
1919. Siebenrock, 275.
1920. Werner, 424, fig. —.
1929. Flower, 25.
1929h. Loveridge, 14.
1930a. Barbour and Loveridge, 770.
1933. Hamerton, 455.
1933m. Witte, 67.
1934a. Mertens and Müller *in* Rust, 8.
1937c. Loveridge, 269.
1937f. Loveridge, 502.
1937b. Monard, 145.
1937. Ruckes, 101, pl. x, fig. 7.
1941. Witte, 106.
1941e. Loveridge, 115.
1942b. Pitman, 214.
1949. Conant and Hudson, 4.
1949. Moyle, 582.
1950. Williams, 551.
1951. Monard, 168.
1952. Aurelio Bassilio, photo facing p. 97 (as *Cinisis*).
1953. Witte, 15.
1954d. Laurent, 296.

1954. Noël-Hume, 73, pl. v.
1955. Cansdale, 89, 103.
1839. *Kinixis denticulata* Hallowell (not of Linnaeus), 161-169, pls. viii-ix.

Common names. Schweigger's Hinged-Tortoise (Flower); *mbulutobe* (on Loango Coast:Pechuël-Loesche).

Illustrations. Both Shaw (1802) and Bell (1827) provide good drawings of the shell of this distinctive species; more recently Siebenrock (1907) figures the entire tortoise, and excellent photographs from life appear in Johnson (1907), Schmidt (1919) and Noël-Hume (1954).

Description. Beak weakly to strongly hooked, unicuspid; edge of jaws not dentate; prefrontal divided longitudinally; frontal large or broken up; upper head shields small, irregular; forelimb anteriorly covered with a few scattered, extremely large, unequal, imbricate or non-imbricate, more or less pointed scutes which on the anterior edge form a longitudinal series of 4 to 5 from elbow to outer claw; claws 5; hinder side of thigh without enlarged tubercles; heel usually without any spurlike tubercle, if present situated low on the heel; claws 4; tail terminating in a horny, clawlike tubercle that is much larger in ♂ ♂.

Carapace flattened dorsally, sides sloping, not or but scarcely to moderately notched in nuchal region, anterior margin strongly expanded and slightly to strongly reverted, spinose in young, posterior margin not expanded, more or less strongly reverted and strongly serrated, spinose in young, rear end in young sloping gradually, in adults more steeply, if vertical only from the middle of the fifth vertebral; dorsal shields concentrically striated, neither swollen nor convex (except as noted below); nuchal absent or rarely present, elongate,[1] occasionally developed on the underside only[2]; vertebrals 5, first broader than long in young, broader than long, as broad as long, or longer than broad in adults, second to fifth broader than long, second broader or subequal to fifth in young, narrower in adults, fifth flat in hatchlings, more or less convex in adults, broader than the costals; costals 4, rarely 3,[3] not or but rarely forming an angle with the

[1] Present in a Nola tortoise (M.C.Z. 44285).

[2] In a Sangmelima specimen (Siebenrock: 1916).

[3] Three in a Landana tortoise whose missing costal was replaced by broadened fourth and fifth vertebrals (Strauch: 1890).

marginals; marginals 11, rarely 12,[1] the anterior much longer than the posterior ones; supracaudal undivided, more or less reverted in both sexes.

Front lobe of plastron very thick, projecting beyond the anterior border of the carapace, openly or deeply notched, bifid; gulars paired; axillaries 3-4, the innermost small, the one or two outermost more or less concealed; inguinal large, in contact with the femoral; hind lobe very short, truncate, not or very broadly notched posteriorly.

Plastral formula: Abd>h>(g, p, f, an, all extremely variable).

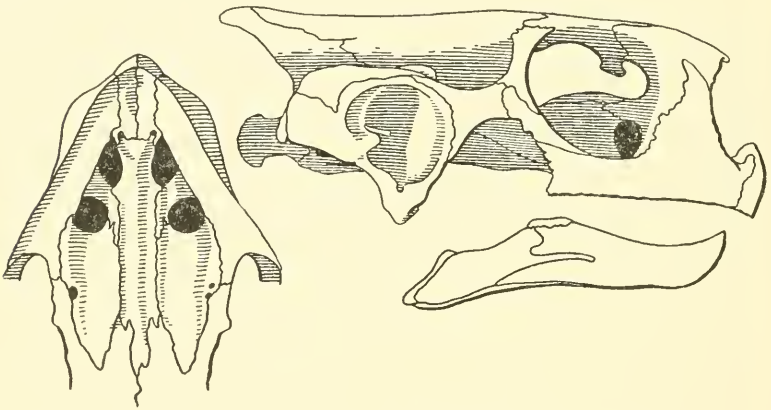


Fig. 48. Skull of *Kinixys erosa* (A.M.N.H. 69727). Condylobasal length 53 mm.

(S. McDowell del.)

For description of a pathological individual, cf. Tornier (1902c).

Color. Carapace of hatchlings pale brown, nearly uniform, darkening with age until almost black while the centers of the shields remain somewhat lighter; in older juveniles and all adults irregularly stellate patches of light yellow appear on the outer margins of the costals, also in smaller areas on the vertebrals, upper portions of the costals and the anteriormost and posteriormost marginals.

[1] Twelve on left side of a Sakbayeme specimen (M.C.Z. 34014).

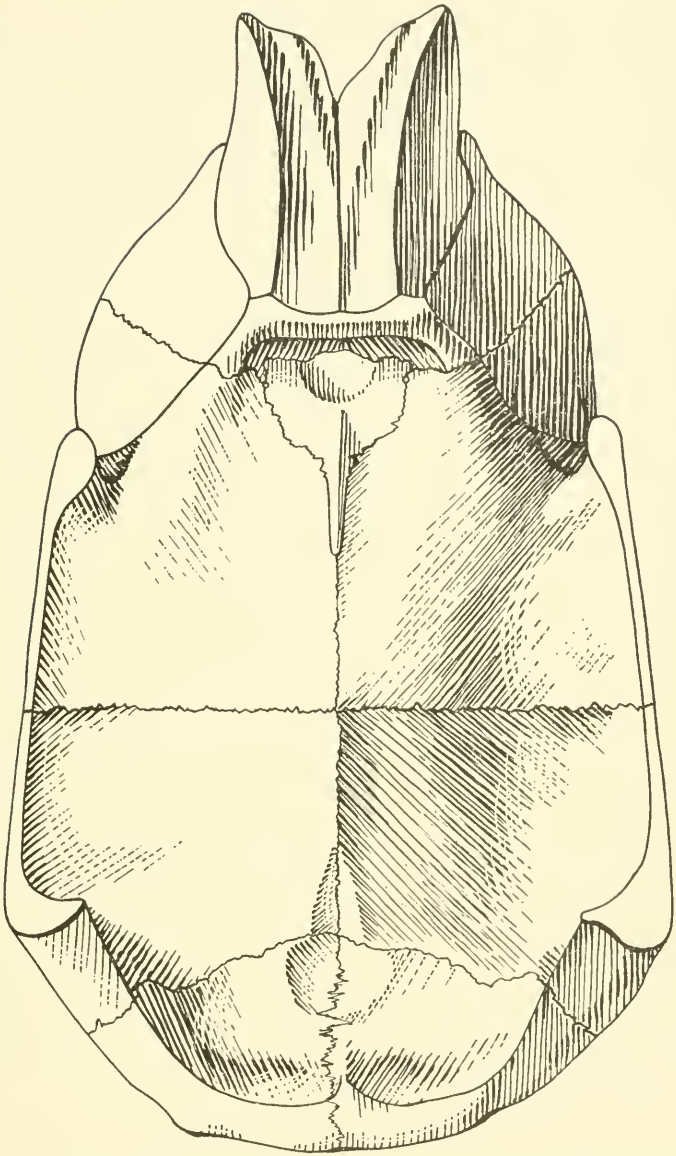


Fig. 49. Internal view of plastron of *Kinixys erosa* (Yale Mus. 4586).
(P. Washer del.)

Plastron yellow, more frequently retained on the gulars than on the remaining shields whose centers are brown or black, sometimes so extensive as to reduce the yellow to narrow lines along the sutures or occasionally a midplastral yellow zone.

Size. Carapace length of largest ♂ (A.M.N.H. 10023), from Banalia, 323 mm., breadth 236 mm., height 122 mm. (Schmidt). Carapace length of largest ♀ (M.C.Z. 52169), from Inferri Chiefdom, 260 mm., breadth 172 mm., height 106 mm.

Sexual dimorphism. The plastron of older ♂ ♂ is more or less concave, their tails considerably longer than those of ♀ ♀.

Breeding. Herbert Lang was told by the Congolese that *erosa* deposits its eggs in sandy ground and covers the site with leaves. One of four eggs laid by a captive tortoise measured 31 x 36 x 40 mm. (Schmidt:1919:406).

Longevity. Three years and five months in Philadelphia Zoo (Conant and Hudson:1949).

Diet. Apparently omnivorous. In captivity one ate apples, pears, sweet potatoes and meat — both raw and cooked (Hallowell:1839). Possibly Büttikofer (1890:436) is repeating native stories when he states that *erosa* eats insects and snails.

Hamerton (1933:455) records a captive tortoise dying of faecal concretions.

Enemies. Eaten by Liberians (Büttikofer) and by Gold Coast natives (Cansdale[1]); also by the inhabitants of the Loango Coast, who convert the shells into ornamental receptacles (Pechuël-Loesche:1882). Eaten also by the Congolese who employ dogs to track the tortoises whose odor betrays them (Lang *in* Schmidt).

Habits. In Liberia *erosa* frequents the shady banks of rivers (Büttikofer). On the Loango Coast Pechuël-Loesche (1882) was informed by the natives that these tortoises actually live in the brooks and rivers, exclusive of tidal estuaries, and bury in the mud. Despite their unwebbed feet they swim well, and captive *erosa* dived to obtain their food in a rather deep basin of water. These aquatic habits, continues Werner (1920), were confirmed by Ussher who informed him that his captive specimen remained in water for as much as a month.

The oft-repeated statement that these tortoises are slow and lethargic, says Kammerer (1908c), is due to captive specimens

[1] In letter of 30.xi.1954.

being subjected to uncongenial conditions such as too little moisture or too low temperatures.

The best account is given by Lang (*in* Schmidt:1919:405), who states that *erosa* "is fond of marshy sites. During the day it hides beneath logs, roots, and heaps of dead and living vegetation, sometimes completely covering itself with debris. The projecting forked gular portion of the plastron and the slightly upturned edges of the carapace are very useful in this task; the head is partly retracted, and the feet then push and wedge until the turtle is hidden from view."

Localities. Uganda: Mabira Forest; Nabea. *Cabinda:* Chinchoxo; Landana. *Belgian Congo:* *Avakubi; Bafwabaka, "Bafwasikuli"[1]; Banalia; Beni; Bikoro; Djalasinda; Duma, Ubangi; Ekibondo; Gamangui; Kabambare; *Kindu (Kindo:U.S.N.M.); Koloka; Kununga; Lake Tanganyika region; "Lissimu"[1]; Masisi in Parc National Albert; Medje (Madie); Niapu; Panga; Poko; *Saidi's Village; Stanleyville; Walikale. *French Equatorial Africa:* Fernan Vaz (Fernand Vas); Gabon; Kama (Camma); Loango; Massabe (Massaba; Massabi); *Nola; *Ntyanga (? Nyanga, or Ntchonga Lake), French Congo (U.S.N.M.); Ogoue (Ogobai). *Rio Muni:* Rio Muni. *French Cameroon:* *Bipindi (C.M.); Campo (or Kampo); Douala; *Efoulen (Efulen); *Kribi; *Lolodorf (C.M.); *Metet (C.M.); Ndikinimeki; *Sakbayeme; *Sangmelima (C.M.); Yaounde (Jaunde). *British Cameroon:* Bonge, Meme River; Buea; Cameroon Mtn.; Johann Albrechtshöhe; Nssakpe; Ossidinge. *Gold Coast:* Aburi; Ankobra (Ancober) River; Ashanti. *Ivory Coast:* Adiopodoume; Yapo Nord (both V.Aellen). *Liberia:* *Bonuta (Bonutah); *Cape Palmas; *Cuttington College, Suacoco; *Harbel; *Lenga, Farmington River; Mesurado River; *Paiata (Peahtah); St. Paul River; *Zorzor. *Sierra Leone:* Barri Chiefdom; *Imferri Chiefdom; *northeast Sierra Leone. *Gambia.* (B.M. 43.2.29.1 and ♂ shell).

Range. Uganda and Belgian Congo northwest to Gambia.

Senegal (Rochebrune) is rejected pending confirmation. Erroneously recorded from North Ameriea (Shaw), Guadeloupe (Duméril and Bibron), and Mozambique (Gray).

[1] In Stanleyville district; a Christy locality (Boulenger: 1919g).

Family TRIONYCHIDAE

1828b. *Trionychidae* Bell, Zool. Jour., **3**, p. 515.

Definition. Cryptodirous testudinates of fully aquatic habit. Horny shields except for obscure rudiments absent, represented by naked skin.

Skull without nasal bones; prefrontals always in contact dorsally, usually with descending processes that are well separated when present; temporal region deeply emarginate posteriorly; parietal never meeting squamosal; postorbital sometimes reduced; quadrate surrounding stapes; post-otic antrum well developed; parietal with well developed descending processes; upper jaw without ridges on its triturating surfaces; vomer usually present, if present short, *not* separating the palatines; mandible with well developed coronoid bone.

Neck vertebrae without a biconvex centrum, all opisthocoelous except the eighth which is doubly convex in front but united to the centrum of the first dorsal only by ligament; entire coracoid blade broad and saber-shaped; tuberosities of humerus widely separated; trochanteric fossa of femur widely open; phalanges with condyles; claws 3.

Carapace not directly united to plastron; carapace not hinged, but plastron with some flexibility between anterior elements; pleural bones always forming a solid disk, but peripheral bones absent (possibly represented by a few ossifications in one genus); nuchal overlapping, or overlapped by, the first pleural, without typical costiform processes or attachment surface for eighth cervical; neural bones hexagonal, mostly short-sided behind, variable in number; pygals absent; plastron with some development of fontanelles; entoplastron absent, mimicked by a separated posterior portion of the epiplastra.

Range. North America; Africa; Asia.

Fossil record. First known from the Lower Cretaceous of Asia (with a possibly ancestral type — *Sinaspideretes* Young and Chow, 1953, Acta Scientia Sinica **2**:226-227, pl. 6 — in the Upper Jurassic or Wealden of the same region). A good record in North America since the Cretaceous; in Europe from Paleocene to Pleistocene. Known in Africa since the Lower Miocene.

Remarks. The trionychids or "soft-shelled turtles"[1] have

[1] A misnomer that has frequently caused misconceptions. Actually in these turtles the carapacial disk is at least as solidly ossified as in other testudinates: only the fleshy margins are soft, except in *Lissemys*, which retains peripherals.

often been separated as one of the major groups within the turtles, coordinate in rank with the Pleurodira, with the marine turtles, and with the land and freshwater forms of more normal or primitive habitus. There are many characters to support such a separation. The peculiar plastron with its callosities and the unique modification of the anterior elements (Williams and McDowell:1952); the skull with its peculiar intermaxillary foramen; the singular fragmented basal plate of the hyoid; the amazing connection of cervical column and dorsal vertebrae (by zygapophyses only); the sickle-shaped scapula; the unique hyperphalangy of the digits; the remarkable penis; the absence of a urogenital sinus, etc., are a formidable complex of features, by any one of which a trionychid may be recognized.

A full analysis of the Trionychidae, setting up phyletic lines and considering carefully both fossil and Recent forms, has not yet been attempted. Yet there are indications such an analysis is less difficult than reputed. It is true that the herpetologist dealing only with externals, is perplexed by the lack of characters he can utilize, and is further disturbed by ontogenetic change (as in the shape and number of the plastral callosities), as well as by individual variation (as in the breadth of the maxillary triturating surfaces). In these turtles, however, even more than in others, it is necessary to go below the surface and, for example, use osteological characters. Consequently for every species we offer two descriptions, one of externals, including color, and a second dealing with its osteological characteristics.

When the osteology is taken into account the African species are remarkably distinct. We have not carried through a study of the osteological characters of the extra-African species, but preliminary explorations by one of us, and by previous workers, convince us of its practicality. Siebenrock (1902b), for example, has demonstrated the usefulness of plastral characters. He presents a key to the living trionychids based entirely on the plastron, also an atlas of plastral bone conformation. Both atlas and key are still very useful. In his key Siebenrock did not emphasize the number or shape of the callosities — very wisely, for it is the latter that (because of individual and age variation) are most likely to make use of his atlas difficult and deceptive. On the contrary, if attention is paid to the shapes and processes of

the underlying bones, the characters employed by Siebenrock successfully separate all but the most closely related species. All the African species are clearly separable by their plastral characters.

The skulls of trionychids, to mention another area of osteological study that has proved rewarding in the African species, have not been exploited sufficiently. More attention has been paid to general shape and to the varying breadth of the maxillary triturating surfaces than to suture patterns and details of morphology which promise to be much more useful.

TABLE 8

Characters of the two sections of the Trionychidae

GROUP I	GROUP II
Trionyx; Pelochelys; Chitra.	*Lissemys; Cyclanorbis; Cyclo-derma.*
Plastron without cutaneous femoral valves.	Plastron with cutaneous femoral valves under which the hind limb may be concealed.
Sculpture characteristically of anastomosing ridges.	Sculpture more often tuberculate.
Nuchal bone without conspicuous ventral ridges, its posterior margin overlying the first pleural (costal bone).	Nuchal bone with a conspicuous ventral ridge on each side extending posterolaterally to underlie the first pleural (costal bone).
Hyo- and hypoplastra distinct.	Hyo- and hypoplastra fused.
Xiphiplastron gripping lateral prong of posteromedial process of hypoplastron.	Xiphiplastron gripping middle prong of the three prongs of the posteromedial process of hypoplastron.
Posterior border of pterygoids without an ascending process that makes sutural contact with the opisthotic.	Posterior border of pterygoids with an ascending process forming a suture with the opisthotic and greatly restricting the fenestra postotica.

Relationships and Grouping of the Living Trionychids

Since no thorough analysis of all living trionychids has been carried out, any discussion of relationships must necessarily be tentative. Nevertheless, it seems advisable to attempt to place the African species in their proper perspective within the family. Our approach is a conservative one. African trionychids, and the family as a whole, fall into two very distinct major groups which have often been separated as distinct subfamilies. The division, very clear-cut, is based on a conspicuous external character and several internal ones, as set out in Table 8.[1]

As Group I contains only a single African representative — *Trionyx triunguis* — it would be out of place here to discuss its subdivisions in detail. Our purpose is merely to indicate the probable position of *triunguis* in our *tentative* arrangement of the group, which may be subdivided as follows:

Subgroup 1. Relatively unspecialized species primarily Oriental in distribution, primitively with a dorsal pattern of large ocelli.

A. Those with a preneural.
   1. *Trionyx hurum*
   2. *T. leithii*
   3. *T. nigricans*
   4. *T. gangeticus*

B. Those with no preneural and with a mandibular symphysial ridge.
   5. *T. formosus*
   6. *T. cartilagineus*

C. Those with no preneural but without a symphysial ridge.
   7. *T. subplanus*

Subgroup 2. Species with highly modified skulls, primarily Oriental in distribution.

1. *Pelochelys bibronii*
2. *Chitra indica*

[1] Siebenrock (1907; 25 footnote) invites attention to a partial restriction of the fenestra postotica in *Dogania* (= *Trionyx*) *subplana* and *Trionyx sinensis* by a *descending* process of the opisthotic. This condition, which we have verified for *Trionyx subplanus*, differs strikingly from the condition in *Lissemys*, etc., in which the pterygoid forms an *ascending* process. However, in some *Trionyx triunguis* (see p. 429 and Fig. 54) the pterygoids may send up an ascending process like that of *Lissemys*, but in this case it fails to make contact with the opisthotic.

Subgroup 3. Relatively unspecialized species primarily extra-Oriental in distribution, primitively without a dorsal pattern of large ocelli.

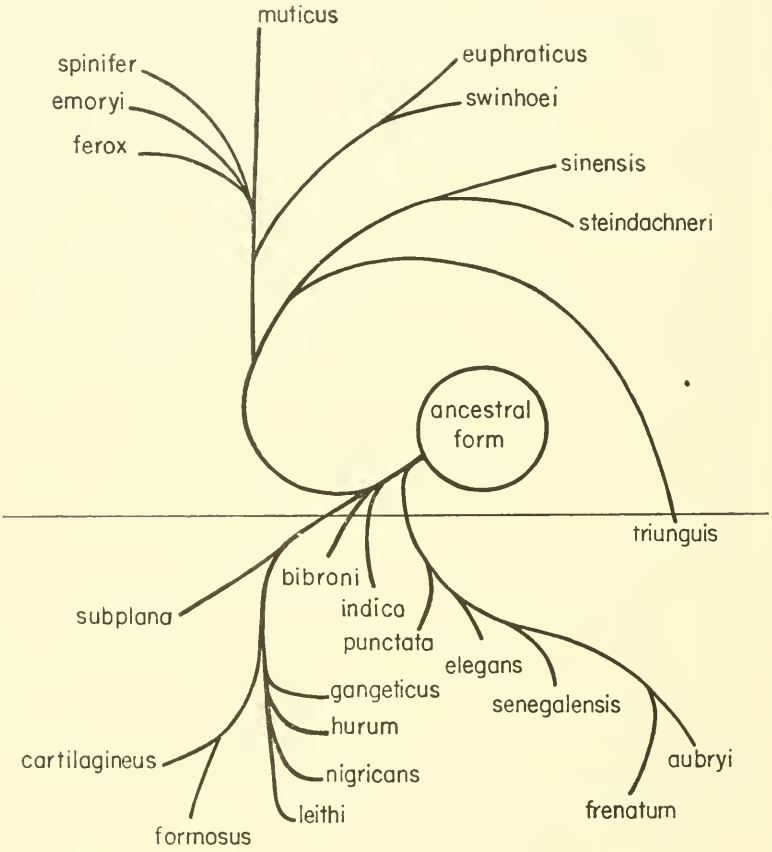


Fig. 50. Dendrogram of trionychid species relationships. The purely hypothetical horizontal line divides those species which may have evolved north of the ancient Tethys sea from those which may have evolved south of it.

(P. Washer del.)

A. Those whose 8th pleurals are typically not reduced.
   1. *Trionyx triunguis*
   2. *T. sinensis*
   3. *T. steindachneri*

B. Those whose 8th pleurals are typically partially reduced.
   3. *T. euphraticus*
   4. *T. swinhoei*

C. Those whose 8th pleurals are typically much reduced or absent.
   5. *T. ferox*
   6. *T. emoryi*
   7. *T. spinifer*
   8. *T. muticus*

This conception of the most probable relationships within the Trionychidae is presented as a dendrogram (see Fig. 50).

Trionyx triunguis, as indicated on the dendrogram, is phyletically quite remote from the other African trionychids. It and they represent two invasions of Africa. Curiously, however, so far as the available fossil record indicates, the two invasions may have been simultaneous. Both groups are clearly represented in the Lower Miocene, which offers the first record of trionychids in Africa.

An overall view of the characters of African trionychids is given in the following table.

In Group II there is, in addition to the two African genera, one Indian genus — *Lissemys. Lissemys,* while clearly a member of the group, seems not to be very closely related to *Cyclanorbis* or *Cycloderma.* From both, as well as from all other trionychids, it differs in the possession of peripheral ossifications (usually regarded as non-homologous with the peripherals of other turtles).

The African members of Group II appear to form a series of their own. Each species has its individual specialization and yet appears to form part of a sequence which, beginning with the most primitive form, is as follows: *Cyclanorbis elegans, C. senegalensis, Cycloderma frenatum, C. aubryi.* Alone of the African series, *Cyclanorbis elegans* retains prefrontal connection with the vomer (primitively present in all turtles; lost, except in this series, only in *Chitra* and the suborder Pleuro-

TABLE 9
Characters of the African Species of Trionychidae

triunguis	*elegans*	*senegalensis*	*frenatum*	*aubryi*
premaxillary bone small but distinct	premaxillary bone small but distinct	as in *elegans*	premaxillary bone apparently absent, at most scalelike	as in *frenatum*
distance from tip of premaxillary to orbit much greater than long diameter of the orbit	distance from tip of premaxillary to orbit less than the long diameter of the orbit	distance from tip of premaxillary to orbit greater than the long diameter of the orbit	distance from tip of premaxillary to orbit subequal to long diameter of the orbit	as in *frenatum*
height of orbit somewhat greater than the interorbital width	height of orbit about twice the interorbital width	as in *elegans*	as in *elegans*	height of orbit about one and one third the interorbital width
prefrontal bones meet the vomer	prefrontal bones meet the vomer	prefrontal bones not meeting vomer	as in *senegalensis*	as in *senegalensis*
intermaxillary foramen large, ovoid	intermaxillary foramen absent	intermaxillary foramen small, narrowed anteriorly	as in *senegalensis*	as in *senegalensis*
prechoanal part of vomer concealed by union of maxillary medial processes	prechoanal part of vomer concealed by union of maxillary medial processes	vomer exposed throughout its entire length or concealed	as in *elegans*	as in *elegans*
jugal enters orbit	jugal enters orbit	as in *elegans*	as in *elegans*	jugal excluded
jugal separated from or only narrowly in contact with the parietal	jugal *narrowly* in contact with the parietal	as in *elegans*	jugal *broadly* in contact with the parietal	as in *frenatum*
neurals 8;	neurals 6-8 +	neurals 1-5 +	neurals 7-8 +	neurals 7-8 +
no preneural	preneural	preneural	preneural	preneural
callosities in adults 4-5.	callosities in adults 2-4	callosities in adults 7-9 or more	callosities in adults 7	as in *frenatum*
sometimes an azygous callosity in gular region	never any callosities in gular region	supernumerary callosities in gular region	callosities on preplastra and fused epiplastra	as in *frenatum*
xiphiplastral callosities always present	xiphiplastral callosities weak or absent	as in *elegans*	xiphiplastral callosities strongly developed	as in *frenatum*
xiphiplastra long, triangular	xiphiplastra posteriorly pointed	xiphiplastra posteriorly broad and notched	as in *senegalensis*	as in *senegalensis*
color of hatchling: head profusely spotted with lighter; throat spotted and vermiculated;	*color of hatchling:* head profusely spotted with yellow; throat vermiculated;	*color of hatchling:* head vaguely mottled; throat immaculate;	*color of hatchling:* head grayish with 5 lines; throat nearly immaculate;	*color of hatchling:* head light brown with 5 lines; throat indistinctly flecked;
carapace olive to dark brown, uniform or much speckled;	carapace green with irregular yellow blotches;	carapace gray-brown vaguely mottled;	carapace gray or green, nearly uniform;	carapace light brownish with a chocolate brown vertebral stripe;
plastron white, immaculate or with dusky vermiculations anteriorly	plastron spotted with yellow to periphery	plastron with a brownish blotch in centre, periphery immaculate	plastron whitish with small black blotches	plastron with two broad V-shaped, chocolate-brown markings, a small one on gular region, a larger one from axillae to teil
size of disk to 950 mm.	size of disk to 440 mm.	size of disk to 350 mm.	size of disk to 470 mm.	size of disk to 330 mm.

dira).[1] *C. senegalensis* lacks the vomer-prefrontal connection but, as in *elegans,* has a narrow postorbital bar. This bar is tremendously broadened in both species of *Cycloderma,* resulting in extensive contact between parietal and jugal, though in primitive fashion *C. frenatum* still retains the jugal entering the orbit. In *C. aubryi* the jugal is excluded from the orbit, thus completing the series of cranial modifications by one that is unique in the family.

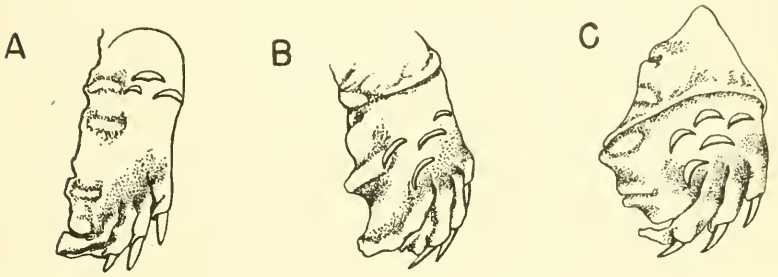


Fig. 51. Forefoot scalation in certain trionychids. *A, Trionyx triunguis* (M.C.Z. 16509); *B, Cyclanorbis elegans* (B.M.); *C, Cyclanorbis senegalensis* (Z.M.U.).

(P. Washer del.)

Key to the Trionychidae of Africa

1. Femoral flaps absent; nuchal somewhat overlapping second rib; hyo- and hypoplastra separate; lateral prong of posteromedial process of hypoplastron gripped by xiphiplastron; pterygoids not joining opisthotic; fenestra postotica not or not much restricted; head spotted. Range: Egypt and Eritrea south to Lake Rudolf, southwest to Lake Albert and Angola, northwest to Senegal.....*Trionyx triunguis* Forskål (p. 3)

   Femoral flaps present; nuchal not overlapping second rib, more or less projecting under second pleural; hyo- and hypoplastra fused; middle prong of posteromedial process of hyo-hypoplastron gripped by xiphiplastron; pterygoids joining opisthotic, greatly restricting fenestra postotica 2

[1] In trionychids the connection is mostly formed by ascending processes of the vomer meeting the prefrontals. In primitive turtles and in many modern forms (e.g. marine turtles), the prefrontal and vomer share about equally in this peculiar bony strut. In testudinids the connection is almost entirely formed from the prefrontals.

2. Head spotted or partly vermiculated, at least in young; postorbital arch narrower than diameter of orbit; preplastra long, angular; no trace of a xiphiplastral commissure .....3 (*Cyclanorbis* Gray)[1]

   Head striped, at least in young; postorbital arch wider than diameter of orbit; preplastra short, straight; a xiphiplastral commissure present ..... 4 (*Cycloderma* Peters)

3. Carapace of hatchlings with large yellow blotches; plastral area with a large dark central blotch profusely spotted with yellow, at least anteriorly; no trace of gular callosities at any age; xiphiplastra pointed posteriorly; prefrontal bones meeting vomer. Range: Sudan; Nigeria; Togo .....*Cyclanorbis elegans* Gray (p. 438)

   Carapace of hatchlings with small black spots; central plastral area more or less blotched with dark; gular callosities, 4 or more in adults, present even in the halfgrown; xiphiplastra broad and notched posteriorly; prefrontal bones not meeting vomer. Range: Sudan west through French Cameroon to Senegal .....
   C. senagalensis (Duméril and Bibron) (p. 443)

4. Carapace of hatchlings orange or orange brown with a narrow black vertebral line anteriorly; jugal bone excluded from orbit; in adults the azygous callosity is subcircular, large; hyo-hypoplastral callosities in contact with xiphiplastral callosities by long straight sutures. Range: Portuguese, French, and adjacent rivers of western Belgian Congo .....*Cycloderma aubryi* (Duméril) (p. 453)

   Carapace of hatchlings pale gray or leaden[2] without a vertebral streak; jugal bone enters orbit; in adults the azygous callosity is crescentic, suberescentic or semilunar, and smallest of all the callosities; hyo-hypoplastral callosities separated from, or in contact with the xiphiplastral callosities by only a short suture. Range: Tanganyika Territory (Rovuma River and Lake Nyasa) southwest through Nyasaland (Lake Nyasa and Shire River) to Mozambique (Zambezi River and affluents) .....*C. frenatum* Peters (p. 459)

Genus TRIONYX Geoffroy

1809a. *Trionyx* Geoffroy, Ann. Mus. Hist. Nat. (Paris), **14**, p. 1. Type by original designation: *Trionyx aegyptiacus* = *Testudo triunguis* Forskål.

1830. *Aspidonectes* Wagler, Natür. Syst. Amphib., p. 134. Type by Stejneger's designation: *Trionyx aegyptiacus* Geoffroy = *Testudo triunguis* Forskål.

1835. *Gymnopus* Duméril and Bibron, Erpét. Gén., **2**, p. 472. New name for *Aspidonectes* Wagler.

[1] A single juvenile specimen from the northwest shore of Lake Tanganyika will not key out even generically on the characters here used and may be a new form. See page 450.

[2] Green in Zambezi turtles according to Peters (1822a, pl. 1).

1835. *Platypeltis* Fitzinger, Ann. Wiener Mus., **1**, pp. 109, 120, 127. Type by Fitzinger's 1843 designation: *Testudo ferox* Schneider.

1835. *Pelodiscus* Fitzinger, Ann. Wiener Mus., **1**, pp. 110, 120, 127. Type by Fitzinger's 1843 designation: *Trionyx sinensis* Wiegmann.

1835. *Amyda* Fitzinger, Ann. Wiener Mus., **1**, pp. 110, 120, 127. Type by original designation: *Trionyx subplanus* Geoffroy.

1843. *Potamochelys* Fitzinger, Syst. Rept., p. 30. Type by original designation: *Trionyx javanicus* Wiegmann = *Testudo cartilaginea* Boddaert.

1844. *Tyrse* Gray, Cat. Tortoises Brit. Mus., p. 47. Type by tautonomy: *Trionyx niloticus* Gray = *Testudo triunguis* Forskål.

1844. *Dogania* Gray, Cat. Tortoises Brit. Mus., p. 49. Type by monotypy: *Trionyx subplanus* Geoffroy.

1864c. *Rafetus* Gray, Proc. Zool. Soc. London, p. 81. Type by monotypy: *Testudo euphratica* Daudin.

1864c. *Aspilus* Gray, Proc. Zool. Soc. London, p. 83. Type by original designation: *Trionyx cariniferus* Gray = *Testudo cartilaginea* Boddaert.

1869c. *Landemania* Gray, Proc. Zool. Soc. London, p. 215. Type by monotypy: *L. irrorata* Gray = *Trionyx sinensis* Wiegmann.

1869c. *Fordia* Gray, Proc. Zool. Soc. London, p. 219. Type by monotypy: *F. africana* Gray = *Testudo triunguis* Forskål.

1869c. *Callinia* Gray, Proc. Zool. Soc. London, p. 221. Type by Stejneger's designation: *Trionyx spinifer* Lesueur.

1872. *Nilssonia* Gray, Ann. Mag. Nat. Hist. (4), **10**, p. 332. Type by monotypy: *Trionyx formosus* Gray.

1873. *Isola* Gray, Proc. Zool. Soc. London, p. 51, fig. 2. Type by monotypy: *Trionyx peguensis* Gray = *Trionyx formosus* Gray.

1873. *Ida* Gray, Proc. Zool. Soc. London, p. 55, fig. 7. Type by monotypy: *Trionyx ornata* Gray = *Testudo cartilaginea* Boddaert.

1873. *Oscaria* Gray, Ann. Mag. Nat. Hist. (4), **12**, p. 157. Type by monotypy: *O. swinhoei* Gray.

1880. *Yuen* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 18. Type *fide* Stejneger: *Y. leprosus* Heude = *Oscaria swinhoei* Gray.

1880. *Psilognathus* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 24, pl. ii. Type by monotypy: *P. laevis* Heude = *Trionyx sinensis* Weigmann.

1880. *Temnognathus* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 25, pl. iii. Type by monotypy: *T. mordax* Heude = *Trionyx sinensis* Wiegmann.

1880. *Gomphopelta* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 27, pl. iv. Type by monotypy: *G. officinalis* Heude = *Trionyx sinensis* Wiegmann.

1880. *Coelognathus* Heude (not of Hessling: 1852), Mém. Hist. Nat. Emp. Chinois, **1**, p. 29, pl. v. Type by monotypy: *C. novemcostatus* Heude = *Trionyx sinensis* Wiegmann.

1880. *Tortisternum* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 31, pl. vi. Type by monotypy: *T. novemcostatum* Heude = *Trionyx sinensis* Wiegmann.

1880. *Ceramopelta* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 33, pl. vii. Type by monotypy: *C. latirostris* Heude = *Trionyx sinensis* Wiegmann.

1880. *Coptopelta* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 34, pl. viii. Type by monotypy: *C. septemcostata* Heude = *Trionyx sinensis* Wiegmann.

1880. *Cinctisternum* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 36, pl. ix. Type by monotypy: *C. bicinctum* Heude = *Trionyx sinensis* Wiegmann.

1903. *Aspideretes* Hay, Proc. Amer. Philos. Soc., **42**, p. 274. Type by original designation: *Trionyx gangeticus* Cuvier.

1944. *Euamyda* Stejneger, Bull. Mus. Comp. Zool., **94**, p. 9. New name for *Amyda mutica* Agassiz.

Synonymy. The listing of *Amyda* Schweigger MS in the synonymy of his *Trionyx* by Geoffroy-Saint-Hilaire (1809a:15), neither constitutes the proposal of a new name nor validates it. Nor is *Amyda* validated by its brief mention by Oken (1816: Lehrbuch der Naturgeschichte, Teil 3, Abt. 2, 348). The first acceptable usage would appear to be that of Fitzinger (1835: 120) as listed above, and the first explicit designation of a type species that by Fitzinger (1843:30) — *Amyda subplana.* Since we regard *subplanus* as a species of *Trionyx,* the necessity of substituting *Amyda* Fitzinger, 1836, for the currently used *Dogania* Gray, 1844, does not arise.

In regard to the type of *Trionyx* Geoffroy, we concur with Schmidt (1953, Checklist of North American Amphibians and Reptiles, p. 108) in believing that Geoffroy, when citing *T. aegyptiacus* as giving an *exact idea* of the habitus and generic characters of *Trionyx,* was consciously and with full intent designating the type of that genus. Admittedly the word "type" was not used by Geoffroy, but we must point out that no species except the genotype can give an *exact idea* of the habitus and generic characters of a genus, and that this is the sole function and meaning of a genotype. Furthermore, we invite attention to evidence that Geoffroy's words were accepted as a type

designation by at least one of his contemporaries. Bory de Saint Vincent (1828, Résumé d'Erpétologie ou d'Histoire naturelle des Reptiles [Paris], p. 77) has this to say: "C'est au célèbre professeur Geoffroy de Saint-Hilaire que l'on doit l'établissement de ce genre [*Trionyx*] dont le type fut une très singulière tortue du Nil que nous avons fait représenter dans notre planche 6e."

Definition. Cutaneous femoral flaps absent.

Skull without maxillary ridging; intermaxillary foramen moderate to large; prefrontal always with connection to vomer; jugal not or but scarcely in contact with parietal; postorbital arch narrower than diameter of orbit; pterygoids never joining opisthotic; fenestra postotica unrestricted.

Carapace without prenuchal bone, without peripheral ossifications; nuchal bone not notched laterally, no raised ventrolateral processes, its lateral margin tending to overlie the second rib; between the first pleurals are 1 or 2 neurals; neurals 7 to 9; pleurals 7 or 8 pairs, the last one or two in contact medially.

Plastron with preplastra long and angular; hyo- and hypoplastra separate, the latter's posteromedial process with a prong that is inserted between the two anterior prongs of the adjacent xiphiplastron; callosities variable.

Range. North America; Africa; Asia.

Fossil record. A good record since the Cretaceous. First reported in Africa from the Lower Miocene of Kenya; first recorded in North Africa from the Pliocene; present in the western portion of North Africa in the Pleistocene.

Trionyx triunguis (Forskål)

1775. *Testudo triunguis* Forskål, Descr. Anim. Avium. Amphib., p. ix: Nile River.
1789. Gmelin, 1039.
1792. Schneider, 280.
1809a. *Trionyx aegyptiacus* Geoffroy, Ann. Mus. Hist. Nat. (Paris), **14**, p. 12, pls. i-ii: Nile River, Egypt.
1809b. Geoffroy, 368 (proof of priority over 1809a unobtainable).
1812. Schweigger (part), 286, 328, 364.
1814. Schweigger (part) (reprint of 1812), 16.
1820. Goldfuss, 179.

1820. Merrem, 20.
1824. Mohring (on osteology: not seen).
1827a. Geoffroy, 115, pl. i, figs. 1-1′.
1828. Bory de Saint Vincent, 77.
1829. Bory de Saint Vincent, 2, pl. vi.
1829. Guérin, 6, pl. i, fig. 7 (as *Tryonix*).
1835. Rüppell, 3, footnote.
1856a. Duméril, 377.
1856. Lichtenstein and Martens, 1.
1857. Jan, 36.
1860. Duméril, 168, footnote.
1862b. Peters, 271.
1862a. Strauch, 175.
1865. Strauch, 126.
1870a. Steindachner, 326.
1874. Reichenow, 298.
1877. Bruhl, pl. xxxiii, figs. 9, 13; pl. xxxiv, figs. 7, 10.
1880. Boettger, 208.
1880. Bruhl, pl. lxix, figs. 5-6 (skull).
1880b. Vaillant, 797.
1880c. Vaillant, 54, pl. xxx, fig. 14.
1887. Lortet, 24.
1897. Sjöstedt, 33.
1905. Barbier, 96.
1831c. *Trionyx Niloticus* "Shaw", Gray, Syn. Rept., p. 46: Nile River.
1831b. Gray, 18.
1835. Temminck and Schlegel, 31.
1845b. Rüppell, 298.
1855. Gray, 68.
1867. Baker, 44, 203, 374 (as *Trionis*).
1882a. Müller, F., 164.
1882. Pechuël-Loesche, 277.
1929. Worthington, 123.
1835. *Gymnopus aegyptiacus* Duméril and Bibron, 484.
1851. Duméril and Duméril, 22.
1851. Guichenot, 190.
1867a. Bocage, 218.
1884a. Rochebrune, 31, pl. iii, figs. 1-2.
1884b. Sauvage, 200.
1837. *Trionyx labiatus* Bell, Monog. Testudinata, text to col. pls. — (= xviii-xx): Sierra Leone.
1872b. Gray, p. 11, *in* Sowerby and Lear pls. lii-liv.
1843. *Aspidonectes Aegyptiacus* Fitzinger, 30.

1855. Fitzinger, 252.
1844. *Trionyx Mortoni* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 120: Africa.
1844. *Tyrse nilotica* Gray, 48.
1864c. Gray, 88.
1870e. Gray, 108.
1872e. Gray, 27.
1873b. Gray, 84.
1873g. Gray, 470.
1859. *Aspidonectes aspilus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 295: Ovenga and Rembo Rivers, Fernan Vaz (as Fernando Vas), Gabon.
1869c. *Fordia africana* Gray, Proc. Zool. Soc. London, p. 219: Nile River at Khartoum, Anglo-Egyptian Sudan.
1869b. Gray, 191.
1870. Gray, 100 (reprint of 1869c).
1873. Gray, 43, figs. 1a-1d.
1873b. Gray, 77.
1875a. *Trionyx triunguis* Peters, 196.
1876a. Peters, 117.
1877c. Peters, 611.
1882. Pechuël-Loesche, 277.
1889a. Boulenger, 254.
1889. Hesse, 261.
1890. Büttikofer, 437, 478.
1890. Strauch, 113.
1893a. Boettger, 16.
1893c. Matschie, 208.
1895a. Bocage, 7.
1896. Anderson, 95.
1896c. Boulenger, 17.
1897g. Boulenger, 277.
1897b. Mocquard, 5.
1897. Sjöstedt, 7.
1898. Anderson, 32, col. pl. iii.
1898. Jeude, 10.
1898a. Werner, 204.
1900b. Boulenger, 447.
1901. Gadow, 410.
1901c. Tornier, 68.
1902b. Siebenrock, 826, fig. 8.
1902c. Tornier, 665.

1902a. Werner, 348.
1904. Andersson, 9.
1906. Johnston, 820, 833.
1906a. Mocquard, 481.
1906a. Siebenrock, 827.
1908. Johnston, 929 (generic name only).
1908. Werner, 1826.
1909b. Pellegrin, 413.
1909a. Siebenrock, 600.
1910. Müller, L., 623.
1910. Sternfeld, 7, fig. 16.
1911a. Masi, 37.
1917. Sternfeld, 417.
1923g. Loveridge, 933.
1924b. Loveridge, 3.
1925b. Flower, 935.
1926a. Mertens, 152.
1927. Calabresi, 38.
1928b. Scortecci, 336.
1928b. Witte, 49.
1929. Flower, 51.
1929. Hummel, 376.
1930a. Scortecci, 216.
1932a. Parker, 229.
1933. Flower, 753.
1933m. Witte, 68.
1933. Worthington, 38, 189 (as *Trionix*).
1937a. Flower, 16, 37.
1937f. Loveridge, 489, 495, 503.
1943. Scortecci, 270, 283.
1948c. Cansdale, 71 (as *Trionyx* only).
1948. Deraniyagala, 29.
1950. Williams, 552.
1953. Durrell, 253, fig.
1884a. *Gymnopus aspilus* Rochebrune, 32.
1893. *Pelodiscus triunguis* Baur, 220.
1899. *Leathery tortoises* Ansorge, 289.
1919. *Amyda triunguis* Schmidt, 598, 601.
1930a. Barbour and Loveridge, 770.
1934a. Mertens and Müller *in* Rust, 12.
1940c. Mertens, 236, figs.1-5.
1955. Cansdale, 93, 104, fig. H6.
1948. *Trionyx triunguis rudolfianus* Deraniyagala, Spolia Zeylanica, 25.

part 2, p. 30, fig. 5, pl. xii, fig. c: Ferguson's Gulf, Lake Rudolf, Kenya Colony.

1955. *Amyda triunguis triunguis* Hellmich, 11, 12, 15 (of reprint).

Synonymy. The young soft-shelled turtle, allegedly from the Gabon River, described by Strauch (1890:113, pl. iii, figs. 3-4) as *Trionyx vertebralis,* later proved to be a juvenile *Trionyx subplanus* Geoffroy, according to Siebenrock (1909:606).

Common names. Nile Soft-shelled Turtle (Flower:1929); Soft-shelled River-Turtle (Cansdale); *abibi* (Alua and Gang of West Nile:Pitman MS.); *abu geda* (Arabic on White Nile:Werner); *bekoom* (Liberia:R. P. Currie); *ger* (Alva and Gang for any aquatic turtle: Pitman MS); *gondo* (in Catumbela: Anchieta); *kunda* (Banziri: Johnston); *navingo* (Bagungu of Bunyoro: Pitman MS.); *neko* (Sango: Johnston); *terseh, tirse* or *tyrse* (Arabic: *fide* Anderson, Forskal and Geoffroy respectively; also *cirsé* or *thirsé: fide* Burton); *um diraga* (riverine Arabs: Flower).

Illustrations. Bell's fine colored plates (1837) of this species (as *labiatus*) are reproduced in Sowerby and Lear (1872:pls. liii-liv); equally good are the colored figures in Anderson (1898:pl. iii), reproduced in black and white as our Plate 15.

Description. Proboscis projecting, the distance from its tip to the orbit longer than orbital diameter in both young and adults; nostril with a papilla-like process projecting laterally from the median wall; forelimb with 3 sharp-edged, crescentic skin-folds on its anterior surface and two weal-like skin-thickenings (absent in young) on outer aspect; hind foot with another sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail very short, pointed, not projecting beyond the posterior leathery margin of the carapace.

Carapace of young with an indistinct keel and covered with tubercles arranged in more or less wavy longitudinal lines; carapace[1] of adults smoother in life but showing, when dried, the underlying bony sculpture; leathery margin relatively extensive, posteriorly extending well beyond tail.

Plastron of young smooth, without callosities, which are late in developing (not visible in a specimen [M.C.Z. 53573] with a carapacial length of 217 mm.); in adults absent on preplastra

[1] A kyphotic shell from the mouth of the Catumbela River is mentioned by Mertens (1926a), more fully with illustrations (1940c).

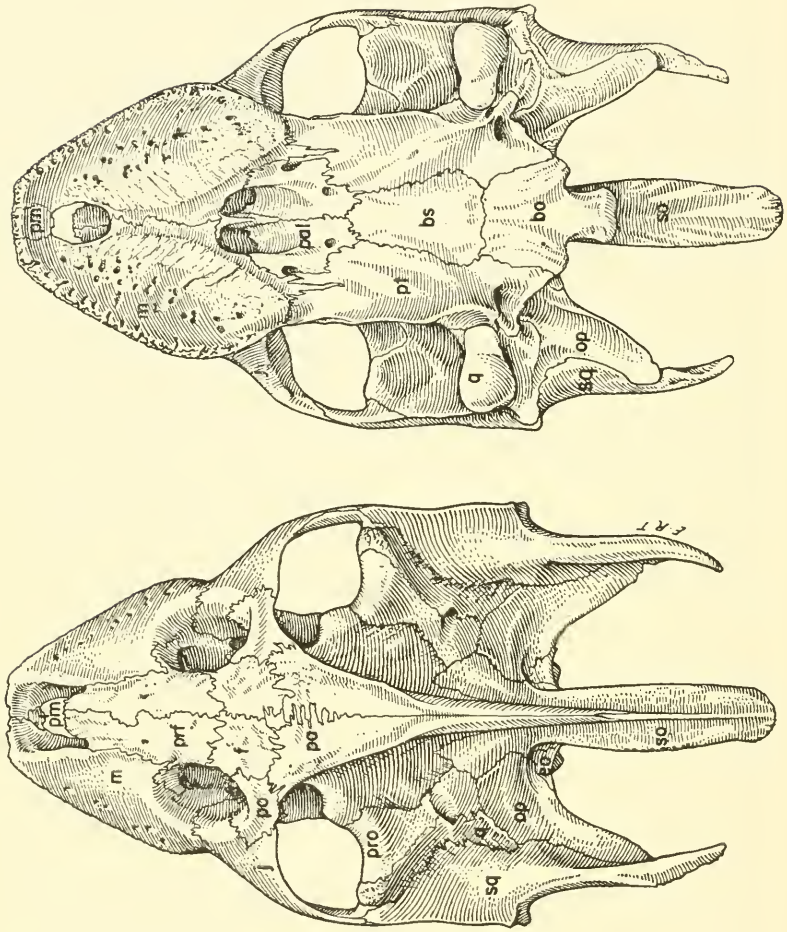


Fig. 52. Skull of *Trionyx triunguis* (B.M. 1947.3.6.12). x ⅔. *Bo* = basioccipital; *bs* = basisphenoid; *eo* = exoccipital; *f* = frontal; *j* = jugal; *m* = maxillary; *op* = opisthotic; *pa* = parietal; *pal* = palatine; *pm* = premaxillary; *po* = postorbital; *prf* = prefrontal; *pro* = prootic; *pt* = pterygoid; *q* = quadrate; *so* = supraoccipital; *sq* = squamosal.

(E. R. Turlington del.)

and the fused epiplastra, present on both hyo- and hypoplastra and on xiphiplastra; anterior edges of the hypoplastral callosities relatively straight; hypoplastral and xiphiplastral callosities not in contact; xiphiplastral callosities not in contact medially; no caudal or femoral flaps but a pronounced crural-caudal skinfold.

Osteological description. Skull. Distance between tip of premaxilla and orbit much greater than the long diameter of orbit; height of orbit greater than the interorbital width, which is subequal to the width of naris; premaxilla single, not separating maxillae underneath the naris, anteriorly bordering a large, ovoid, intermaxillary foramen that is laterally and posteriorly bordered by the maxillae, which are in contact medially for a distance greater than the length of the foramen; vomer stout, in contact with descending processes of the prefrontals, its interchoanal portion relatively short; choanae narrowed, narrower than the least distance between the maxillary triturating surfaces and not bordered by them; postorbital arch not half as wide as the long diameter of orbit; jugal not or but rarely meeting parietal, and then but narrowly; orbit entered by jugal which may, or may not, meet squamosal; squamosal crests thin, sharp, and curving medially; pterygoids sometimes approaching [1] but never meeting opisthotic, not restricting postotic fenestra; mandible without symphysial ridge, its symphysial width equalling or exceeding the long diameter of the orbit.

Carapace. Carapacial bones coarsely pitted and vermiculated; no prenuchal bone; nuchal bone not notched laterally, overlying the second rib; between the first pleurals a single neural; neurals 8; pleurals 8 pairs, the eighth (and sometimes the seventh) wholly or partially in contact medially.

Plastron. Preplastra widely separated, the anterior branch short, about half as long as the posterior; epiplastra fused, forming an acute or right angle; hyo- and hypoplastra distinct, the anteromedial process of the latter with 3 to 5 prongs, medial process broad with several prongs, both medial and posteromedial processes usually united to form an extensive dentate margin;

[1] The pterygoid sends up a triangular, tongue-like process which almost meets the opisthotic in a Lobito Bay turtle (A.M.N.H. 50724) and a second specimen (A.M.N.H. 36599) from "Africa." In another Lobito Bay turtle (A.M.N.H. 50723), as well as in B.M. and M.C.Z. material, this process does not exist.

xiphiplastra very long, triangular, medioanterially united by 2 or 3 prongs inserted into 3 or 4 notches, a long oval fontanelle intervenes in front of the posterior portions which are also in contact.

Callosities 4 (hyo-hypoplastral and xiphiplastral pairs) or 5 (an additional azygous element on the fused epiplastra), sculp-

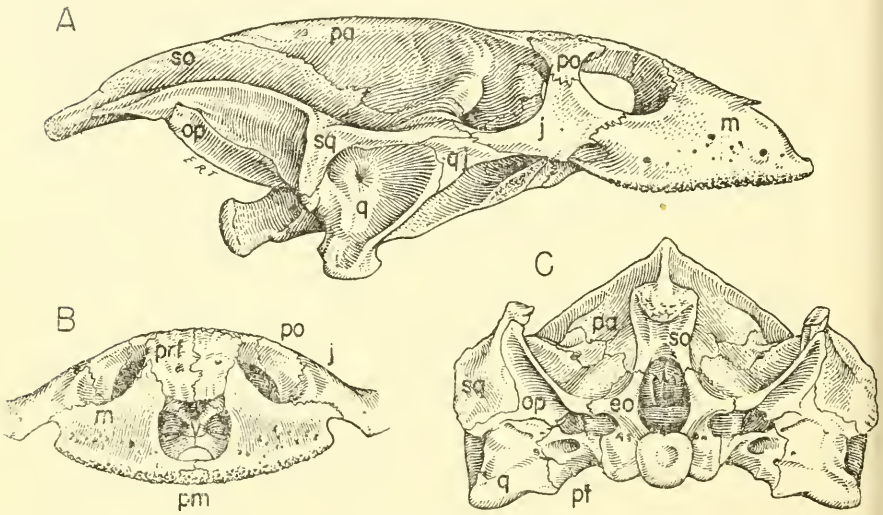


Fig. 53. Skull of *Trionyx triunguis* (B.M. 1947.3.6.12) x ⅔. Letter symbols as in Figure 52 except *v* = vomer. *A*, Lateral view; *B*, anterior view; *C*, posterior view.

(E. R. Turlington del.)

tured like the carapace, well developed but never completely covering the bones.

Color. Carapace olive, dark olive, olive brown or dark brown, uniform or profusely speckled with dark-margined, white (yellow) spots, often well-marked in young, obscure or obsolete in adults; fleshy disk very narrowly edged with yellowish.

Plastral area white or creamy white, immaculate or with coarse, dusky vermiculations anteriorly; fleshy underside of disk dark, laterally with large, dark-bordered, light spots tending to become much smaller posteriorly, also edged with yellowish, either narrowly or presenting a scalloped appearance.

Head and limbs above dark, profusely spotted with lighter; throat of young dark with larger spots and vermiculations, of adults immaculate white or yellow; limbs below lighter, uniform, spotted, or vaguely vermiculate.

Size. Over-all measurements are discarded on account of the extensile neck. It is not clear whether Anderson (1898), when stating that this turtle "attains to a metre in length," was referring to over-all or carapace length. Carapace length of largest [1] 950 mm., from Gaboon River (A.H.A. Duméril:1860:169); another with a length of 800 mm. was taken in Lake Albert (Witte:1928b); a third was 780 mm., breadth 570 mm., from Lake Fisherman (Büttikofer:1890); a Nile specimen of 680 mm.,

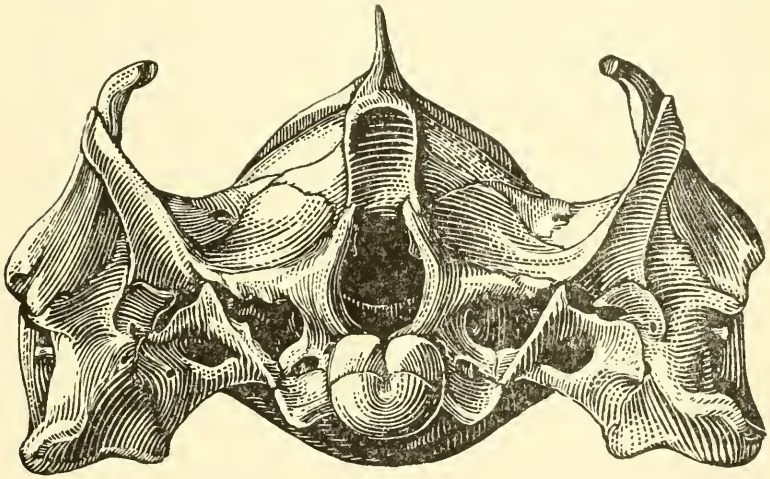


Fig. 54. Skull of *Trionyx triunguis* (A.M.N.H. 36599). Occipital view to show the occasional presence of pterygoid ascending processes.
(S. McDowell del.)

breadth 540 mm., was caught near Duem (Siebenrock:1906a).

A ♂ from Khartoum measured 630 mm., a ♀ from Giza 700 mm. (Flower:1933).

Weight. Largest of sixteen turtles taken in Lake Albert by Worthington (1929) weighed 80 lbs. (as 37 kilos.). The 950 mm.

[1] If this is Duméril's meaning when he says: "sa longeur totale est de 1 m. 33: le bouclier seul a 0 m. 95."

triunguis from the Gaboon weighed 65 lbs. (as 29.7 kilos.), yet the 780 mm. specimen from Lake Fisherman was 75 lbs. Possibly Baker (1867:44), who estimated the weight of one that he hooked (but which escaped before being landed) as "at least 100 lbs." is the source of Worthington's mentioning this weight (1933), but we do not know the basis for that of Mocquard (1906a), who puts the weight of this species as about "100 kilograms," i.e. 220 lbs.!!

Breeding. On March 13, 1928, a ♀ from Butiaba held 27 eggs with shells, measuring rather more than an inch in diameter; there were possibly 100 more about half that size developing in the ovary (Worthington:1929). During April, in Egypt, from 50 to 60 eggs are laid in a sandbank where they are hatched by the solar heat (Anderson:1898). On July 10, 1825, Rüppell observed a *triunguis* on an island in the Nile. The reptile was gently scraping the sand on the upper part of a steep bank. There, three inches below the surface, she deposited 29 spherical eggs, each having a diameter of about 1¼ inches (as 16 lines). The eggs were removed to the ship where, after only two hours, a single young one broke through the shell and began immediately to swim in a basin of water (Rüppell:1835:3).

Longevity. Twenty-five and a half years; another, still alive on 16.ix.36, had been in the London Zoo for 22 years, 1 month, 17 days (Flower:1937a).

Diet. Stomachs of the soft-shelled turtles captured by Rüppell (1835) held nothing but vegetable matter, viz. fragments of dates, gherkins and pumpkins. The reptiles came ashore at night in search of such food, according to local fishermen, who averred they would not take meat bait. This was confirmed by Rüppell's experience, for none took his meat bait but two were hooked when bread-dough was used. The stomachs of two turtles taken in Liberia contained many palm nuts; these Büttikofer (1890) thought they must procure on shore. Anderson (1898:33) thinks it highly improbable that "so thoroughly an aquatic animal as *Trionyx* should leave the water in search of food," and with Flower (1933), apparently regards Arab statements as to *triunguis* digging up and devouring crocodile eggs or hatchlings, as unproven. The allegation that they eat hatchling crocodiles dates back at least to Goldfuss (1820).

Anderson (1898) states that shellfish and fish appear to form their staple food, and these are eaten under water. Worthington (1929) agrees that mollusks and fish, both living and rotting, constitute their principal food, but from one he recovered scraps of goatskin and feet, from another ten large dragonfly nymphs.

Flower (1933), when feeding captive *triunguis* on live bolti fish (*Tilapia*), observed that if a turtle seized a fish in its jaws that was too large to be swallowed whole, it impaled the fish on its foreclaws, tore off the head, and employed its forefeet in finishing the meal. One captive ate ham (Hesse:1889); more unfortunate was the type of *labiatus* which refused all food and died after three weeks (Bell:1837).

Enemies. Being regarded as a delicacy, the Nile Soft-shelled Turtle has been hunted for hundreds, possibly thousands of years, yet a few manage to survive in Egypt. In the Sudan certain natives specialize in the capture of these reptiles when they come ashore to lay their eggs (Flower:1933). References in the literature reveal that the species is preyed upon by Africans in many parts of its range. In the Gold Coast they are sometimes taken in cane fish traps, or the larger turtles are hooked by bottom fishers (Cansdale:1948e).

Durrell (1953) reports that the flesh, when stewed, was "most palatable," tasting "like a rich and slightly oily veal." Baker (1867:374), who removed upwards of a hundred eggs from one of the turtles he hooked, regarded the flavor of resulting omelettes as "rather strong."

Near Kasenyi, Lake Albert, Africans do not eat *triunguis* — possibly for superstitious reasons — and allegedly release any turtles that become entangled in their nets, as P. Janseens informed Dr. J. P. Chapin (*fide* label of vii.1937 on A.M.N.H. 60263).

By stretching the untanned skin of a fish over a turtle carapace, Africans convert it into a guitar (Baker:1867:203). Anderson (1898:33:footnote) quotes Prospero Alpini as saying, in 1735, that the larger carapaces were utilized for making shields, and adds that the practice still persisted in Nubia.

Defense. Sir Samuel Baker (1867:44) relates how, using a strip of glistening perch on a stout hook fitted to treble-twisted wire, he caught an enormous turtle "at least 100 lbs. weight."

However, when his Arab assistant drew the reptile, struggling and snapping, close to the steep bank, its jaws cut through the triple brass wire as with shears.

Durrell (1953) states that the jaws of a decapitated turtle snapped on, and splintered, a piece of wood. Hesse (1889) writes of one snapping at his fingers. According to Bell (1837) the movable and extended coriaceous margin of the carapace enabled the type of *labiatus* to conceal itself in very shallow mud in much the same manner as would a flounder or plaice.

Temperament. Vicious and always ready to bite (Cansdale: 1948c).

Habits. Soft-shelled Turtles run extremely fast when taken out of the water, according to Baker (1867:374) who landed three. A ♀ in the Giza Zoological Gardens frequently travelled from one pond to another. To do so she had to climb a metre-high, vertical fence of wire netting and, after gaining the top, flop down on the farther side (Flower:1933). A very small turtle surprised Worthington (1933:38) by climbing from a bucket. He describes them as wallowing in the crater lakes of an island in Lake Rudolf, where he landed a fifty-pounder accidentally hooked by one of its feet. When occasion demands, however, these turtles can swim fast in their chosen element (Hesse:1889).

Habitat. Ponds, lakes and rivers, but Auguste Duméril (1860: 168:footnote) records a *triunguis* with a carapace length of 950 mm., and weighing 29.7 kilograms, as having been taken in the ocean about 3 or 4 km. from the mouth of the Gaboon River. The collector did not believe such an able swimmer as *Trionyx* could have been carried so far by the river in flood.

However, Flower (1933:754) believes that when the Nile is in spate these turtles are carried into the Mediterranean along with the carcasses of cattle and donkeys, and so up the Palestine coast by the powerful inshore current.

Localities. Egypt:[1] Embaba district, Giza Province; Ezbet Semeda Saleh, Fayum Province; Kom Ombo, Aswan Province; Nile near Cairo; Philae; Wadi Halfa. *Sudan:* *Atbara village (U.S.N.M.); Berber Province; Blue Nile; Delladilla, deep in Base; Dongola; Duem; Halfa Province; Khartoum; Kulgeila,

[1] For discussion of questionable records, see Flower (1933).

Dongola Province; Roseires (Rosairos in B.M.), Blue Nile; Sennar; Shandi; *Sul River; Upper Nile (1873). *Eritrea:* Asmara; Setit River (Fiume). *Ethiopia:* (as Abyssinie:1851) Lake Tana (Zana). *Somalia:* Ganana; Lugh. *Uganda:* Butiaba, Lake Albert. *Kenya Colony:* Ferguson's Gulf, Lake Rudolf; Kaliokwell River Mouth, Lake Rudolf. *Angola:* Benguela; Cuanza; *Cunga; Catumbela; Loanda; *Lobito Bay (A.M.N.H.). *Cabinda:* Chinchoxo. *Belgian Congo:* *Congo River at Lukolela (A.M.N.H.); *Lake Albert at Kasenyi (A.M.N.H.); Mahagi Port; Mayombe (Mayumbe). *French Equatorial Africa:* Bilchem; Fernan Vaz (Fernand Vas); *Gabon River; Kuilu River below Bumina; Lambarene; Loango Coast; Ogoue (Ogowe); Ovenga River; Rembo River. *French Cameroon:* Dibongo, near Edea; Lake Ossa; *Sakbayeme. *British Cameroon:* Bonge, Meme River; Lake Soden; Ossidinge. *Togo:* Kete Krachi (Kratje). *Gold Coast:* Accra; Birrim, tributary of Pra River. *Liberia:* Fisherman Lake; Grand Bassam (G. Massam); *Saint John River near Gbanga; Saint Paul River near Muhlenberg Mission, Mt. Coffee. *Sierra Leone:* *Wanje River near Gbap; *near Kale; *near Subu. *Portuguese Guinea:* Bissao (Bissau). *Gambia. Senegal:* Dagana (1870). *French West Africa:* Bilchem on Niger-chad frontier.

Range. Egypt and Eritrea south to Lake Rudolf, southwest to Lake Albert and Angola, northwest to Senegal. Accidental along Palestine coast of Asia Minor (cf. Flower:1933).

Erroneously included in the fauna of Lake Victoria by Loveridge (1924b) on the basis of alleged remains in the Miocene deposits of Karungu Bay, Lake Victoria, for, as pointed out by Worthington (1929) no living *triunguis* has been taken above the Murchison Falls, White Nile.

Werner (1924a:269), unaware of any record for *triunguis* above Duem on the White Nile, suggests that it occurs only in the lower and middle reaches of that river, besides the entire length of the Blue Nile. Werner makes no mention of its presence in Lakes Albert and Rudolf, and thinks that in the Upper Nile, Sobat River, and Bahr el Ghazal, *Trionyx* is replaced by *Cyclanorbis.*

Genus CYCLANORBIS Gray

1854. *Cyclanorbis* Gray, Proc. Zool. Soc. London, 1852, p. 135. Type: *petersii* Gray (by monotypy) = *senegalensis* (Duméril and Bibron).

1856. *Cyclanosteus* Gray, Proc. Zool. Soc. London, 1855, p. 201. Type: *petersii* Gray (designation by Günther 1865, in Zool. Rec. for 1864).

1865e. *Tetrathyra* Gray, Proc. Zool. Soc. London, p. 323. Type: *petersii* Gray (by monotypy).

1870e. *Baikiea* Gray (not *Baikia* Gray: 1865), Suppl. Cat. Shield Rept., Part 1, p. 114. Type: *elegans* Gray (by monotypy).

Definition. Cutaneous femoral flaps present, permitting concealment of the hind limbs.

Skull without maxillary ridging; intermaxillary foramen small or absent; prefrontals with or without connection with the vomer; jugal narrowly in contact with parietal; postorbital arch narrower than diameter of orbit; pterygoids joining opisthotic, greatly restricting fenestra postotica.

Carapace with prenuchal bone present or absent, without peripheral ossifications; nuchal bone not notched laterally, ventrally with raised posterolateral processes which tend to underlie the first pleurals, between which are two neurals; neural number variable; pleurals 8 pairs, one to all meeting medially.

Plastron with preplastra long and angular; hyo- and hypoplastra fused, their posteromedial process with 3 prongs between which are inserted the 2 anterior prongs of the adjacent xiphiplastron; callosities variable in number, present or absent on gulars.

Range. Southern Sudan west to Senegal.

Fossil record. No fossils certainly identifiable; however, see under *Cycloderma*. The fragment reported by Dacqué (1912: Geol. Pal. Abhandl.:14:322) is at present indeterminable, as Siebenrock suggested when consulted by Dacqué.

Remarks. Both in skull and shell, as a glance at the table on p. 418 will show, the two species of *Cyclanorbis* are strikingly different. These differences, however, reflect the relative primitiveness of *elegans* and relative specialization of *senegalensis*, but the two are still closer to one another than to any other African trionychids. Nevertheless, should it ever seem desirable to separate them generically, the name *Baikiea* Gray is

available for *elegans* while the type of *Cyclanorbis* is *senegalensis*.

C. senegalensis offers no problems at the species level, though ontogenetic changes in the callosities induced Gray to propose names which he very soon synonymized. On the other hand, our identification of *oligotylus* with *elegans* clarifies a muddle of names that began in 1864 when Gray described and figured a skull from Gambia as being possibly that of an adult *senegalensis*. Later Gray associated this skull and similar ones with the mottled juveniles which he described as *Baikiea elegans*. This action was reversed by Boulenger (1889a:272) who returned the skulls to *senegalensis*, restricting *elegans* to the two young cotypes described by Gray. In consequence, Siebenrock (1902b:810), accepting Boulenger's verdict without seeing the British Museum skulls, described a new species *oligotylus*, based on an adult shell.

The persistence of this confusion till the present, is largely attributable to the absence of an adequate ontogenetic series. While there is still no such series of this species, more material is now available and the situation in the freshwaters of north central Africa appears to be as follows:

In this region, so far as is known, there are *only two* kinds of juvenile trionychids with femoral flaps. The two are readily distinguished by color and pattern. One of these is clearly *elegans*, the other is definitely *senegalensis*.

So far as known, there are *only two* kinds of adult cyclanorbide shells from this region. They differ in maximum size, number of neurals [1] (and correspondingly in the number of pleurals in contact), the extreme development of callosities in one versus their great reduction in the other. One corresponds to Siebenrock's description of *oligotylus*, the other is definitely *senegalensis*.

Similarly there are *only two* kinds of adult cyclanorbide skulls known from this region. The larger are clearly referable to *oligotylus* but are also identical with the large skulls which

[1] We consider that size in conjunction with the neural number is a good guide for the separation of the two species. Thus Werner's Mongalla collections reported on by Siebenrock (1906a) and Werner (1924a) separate readily into two series — all the large shells having 6 or more neurals, all the smaller ones 5 or less. Neural number does not increase during ontogeny.

formed part of Gray's concept of *elegans;* the smaller are definitely *senegalensis.*

At each age level there is therefore good evidence for the existence of *only two* cyclanorbide turtles in north central Africa. This has become increasingly clear over the years and the newer collections have been identified on this basis. Thus for some time the British Museum has been labeling its strongly mottled cyclanorbide juveniles *oligotylus,* correctly assuming that they were juveniles of the large adults they had also received. It is only because no comparison with the juvenile cotypes of *elegans* was made that the identity of *oligotylus* and *elegans* has remained so long undiscovered.

Cyclanorbis elegans (Gray)

1864c. *Cyclanosteus senegalensis* (adult ?), Gray (part: omit figs. 16-18 only), 97, figs. 19-21.
1865d. *Tetrathyra baikii* Gray (part: omit shell), 205.
1865e. Gray (part: omit shell), 324 (reprint of 1865d).
1869c. *Baikica elegans* Gray, Proc. Zool. Soc. London, p. 222, pl. xv, fig. 2: Africa (West ?).
1870c. Gray (part: omit *C. senegalensis* var. *callosa*), 114, fig. 39.
1873. Gray, 69.
1873b. Gray, 86.
1889a. *Cyclanorbis elegans* Boulenger, 272.
1909a. Siebenrock, 594.
1919. Schmidt, 601.
1934a. Mertens and Müller *in* Rust, 12.
1889a. *Cyclanorbis senegalensis* Boulenger (part: not of D. and B.), 272 (cotypes r, s, t of *Baikica elegans*).
1897. Siebenrock, 248, pl. ii, fig. 5; pl. iv, fig. 20.
1901c. Tornier, 68 (material lost, but agrees with *elegans* with possible exception of Jeudi specimen).
1902b. *Cyclanorbis oligotylus* Siebenrock, Sitzb. Akad. Wiss. Wien, 111, pp. 810, 842, fig. 17: Nubia (Upper Nile?).
1905a. Siebenrock, 465, fig. 2.
1906a. Siebenrock, 838, fig. 8.
1908. Werner, 169.
1909a. Siebenrock, 594.
1912b. Werner, 493.
1919. Schmidt, 601.
1924a. Werner, 269.
1934a. Mertens and Müller *in* Rust, 12.

Synonymy. Further citations of "*baikii* (part)" will be found under *Cyclanorbis senegalensis.*

Common name. Nubian Soft-shelled Turtle.

Description of hatchling.[1] Proboscis projecting, the distance from its tip to the orbit (not eye) greater than the orbital diameter; upper lips meeting in front to form a flat arch; nostril with a papilla-like process projecting from the median wall; forefoot with 4, sharp-edged crescentic skinfolds on its upper surface, another indistinct weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary, not projecting beyond the posterior rim of the carapace.

Carapace of hatchling with a moderate vertebral keel and numerous, raised, rather wavy, longitudinal lines comprised of small individual tubercles anteriorly converging towards a strongly tubercular nuchal area; leathery margin posteriorly smooth, not extensive, scarcely extending beyond the tail.

Plastron of hatchling smooth, without callosities, femoral (but no caudal) flaps permit concealment of hind limbs.

Osteological description. Skull. Distance between tip of premaxilla and orbit greater than the long diameter of orbit; height of orbit about one and one-third to one and one-half times the interorbital width, which is less than the width of naris; premaxilla single, not separating maxillae underneath the naris; behind the premaxilla the maxillary triturating surfaces meet, their inward extensions closing or partly closing over the intermaxillary foramen; behind the triturating surfaces more dorsal flanges of the maxillae meet mesially ventral to the vomer for a distance greater or less than the palatal length of the premaxilla; vomer slender, in contact with the prefrontals, its interchoanal portion moderately long; choanae only slightly narrowed by inward extensions of the triturating surfaces of the maxillae; postorbital arch somewhat more than half the long diameter of the orbit; orbit entered by jugal, which is narrowly in contact with the parietal; squamosal crests long, sharp, straight or incurved; pterygoids meeting opisthotic, greatly restricting postotic fenestra; mandible without symphysial ridge, its ventral symphysial width less than the diameter of the orbit.

[1] Based on a Khartoum specimen (B.M. 1909.3.25.3).

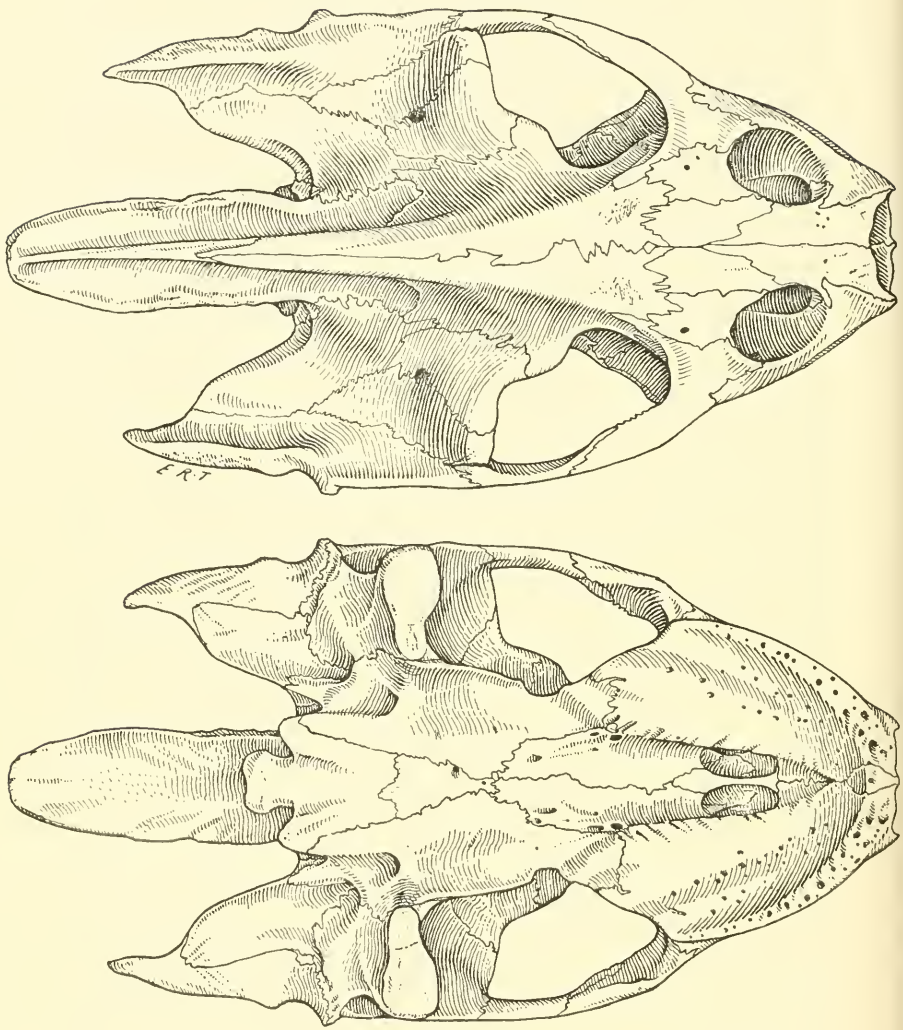


Fig. 55. Skull of *Cyclanorbis elegans* (Cotype. B.M. 65.5.9.22 = 1947. 3.6.28), x ⅔. Dorsal and ventral views.

(E. R. Turlington del.)

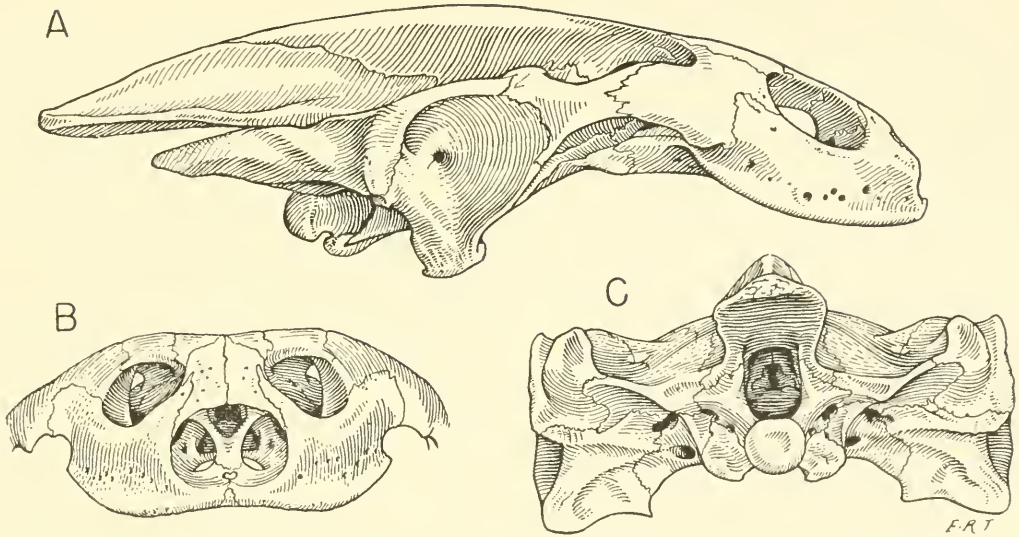


Fig. 56. Skull of *Cyclanorbis elegans* (Cotype. B.M. 65.5.9.22 = 1947. 3.6.28), x ⅔. *A*, Lateral view; *B*, anterior view; *C*, posterior view.
(E. R. Turlington del.)

Carapace. Carapacial bones distinctly granulated; no prenuchal bone; nuchal bone not notched laterally but with multiple digitations underlying to a small extent the first pleurals, between which are two neurals; neurals 8 or 9, forming a continuous series, or the last two separated; pleurals 8 pairs, the eighth in contact medially.

Plastron. Preplastra widely separated, the anterior branch long, longer than the posterior; epiplastra fused, forming an acute angle; hyo- and hypoplastra fused, their anterior border straight or somewhat concave, *not* convex, posterior border of this compound bone very deeply excavated, anteromedial process with indistinct prongs; medial process short, only slightly projecting, posteromedial process with only 3 prongs between which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra rodlike, anteriorly broader, nowhere in contact though converging posteriorly, neither notched nor broad but pointed posteriorly.

Callosities 2 or 4, sculptured like the carapace; usually 2 on the hyo-hyoplastra only, covering most of these bones but widely separated medially; occasionally small callosities on the xiphiplastra.

Color. Carapace of hatchling[1] dark olive brown with large irregular blotches of yellow, the periphery sometimes with a few, scattered, somewhat smaller, roundish, yellow spots. Carapace of adults light brown to olive green, the periphery spotted and vermiculated with light green.

Plastron of hatchling yellowish, its central area dark, profusely spotted with lighter, not, or only sometimes, extending to the periphery; fleshy underside of disk edged or spotted with yellow. Plastron of adults dirty yellow, obscurely blotched with darker.

Head and neck of hatchling gray brown above, anteriorly spotted with lighter, posteriorly darker and unspotted; chin and throat anteriorly vermiculated; neck below, yellow, immaculate; limbs uniform or mottled with yellow. Head of adults above dark brown with light green vermiculations; temporal region olive green; neck lighter, speckled and spotted with yellow; throat and neck below, uniformly yellow.

[1] Checked by a Khartoum specimen (B.M. 1909.3.25.3) with carapace length of 67 mm., and breadth of 50 mm.

Size. Carapace length, including fleshy margin, of *oligotylus* type, 605 mm., its breadth 465 mm., its height 150 mm.; disk of same specimen 440 mm., breadth 400 mm.; exceeded by a dorsal disk from Mongalla with a length of 490 mm. (Siebenrock:1906).

Enemies. At Mongalla, on the Bahr el Jebel, thirteen *Cyclanorbis* carapaces, representing both species, were purchased by Werner, but he could not get the Bari tribesmen to part with an entire turtle. Even the plastron and fleshy margins were sought after for culinary purposes (Siebenrock:1906).

Localities. Sudan: Bahr el Jebel at Mongalla; Nubia; Sobat River at Khor Attar; Upper Sobat at Nasser; White Nile at Khartoum and at *Tonga. *French Equatorial Africa:* Schari River near Fort Archambault (V.M.). *Nigeria:* Niger River at Lohata, Kabba Province. *Togo:* Kete Krachi (Kratje); Mango (Mangu); Yendi (Jendi).

Range. Sudan; Nigeria; Togo.

Cyclanorbis senegalensis (Duméril and Bibron)

1835. *Cryptopus Senegalensis* Duméril and Bibron, Erpét. Gén., **2**, p. 504: Senegal.
1851. Duméril and Duméril, 23.
1844. *Emyda senegalensis* Gray, 47.
1855. Gray, 64.
1860e. Gray, 316.
1854. *Cyclanorbis Petersii* Gray, Proc. Zool. Soc. London, 1852, p. 135: Gambia River, Gambia.
1855. Gray, 69.
1855. *Cyclanosteus Petersii* Gray, 64, pl. xxix.
1860e. Gray, 315.
1860. *Cycloderma senegalense* Duméril, 168.
1865. Strauch, 131.
1862a. *Cycloderma Petersii* Strauch, 56.
1864c. *Cyclanosteus senegalensis* Gray (part: omit figs. 19-21), 95, figs. 16-18.
1870d. Gray, 717, pl. xliii.
1872c. Gray, 27.
1873. Gray, 70.
1873b. Gray, 87.
1884a. Rochebrune (ignored).
1865d. *Tetrathyra baikii* Gray (part: omit young and skulls), Ann. Mag. Nat. Hist. (3), **16**, p. 205, fig. —: ? Niger River, West Africa.

1865e. Gray, 324, fig. — (reprint of 1865d).
1873. Gray, 70.
1873b. Gray, 86.
1884a. Rochebrune, 35 (ignored).
1865f. *Cyclanosteus senegalensis* var. *equilifera* Gray, Proc. Zool. Soc. London, p. 423, fig. 2: Niger River, West Africa.
1870e. Gray, 113, fig. a.
1865f. *Cyclanosteus senegalensis* var. *normalis* Gray, Proc. Zool. Soc. London, p. 423: Niger River, West Africa.
1865f. *Cyclanosteus senegalensis* var. *callosa* Gray, Proc. Zool. Soc. London, p. 423, fig. 1: Niger River, West Africa.
1870e. Gray, 113, fig. 38.
1884a. *Tetrathyra vaillantii* Rochebrune, Faune Senegambie, Reptiles, p. 36, pl. iv, figs. 1-2: Senegal (localities unreliable).
1889a. *Cyclanorbis senegalensis* Boulenger (part: omit *Baikiea elegans* cotypes), 271.
1898. Siebenrock, 425.
1899. Siebenrock, 566.
1900. Flower, 967.
1902b. Siebenrock, 839, fig. 16.
1905a. Siebenrock, 467.
1906a. Siebenrock, 835, fig. 7.
1908. Werner (1907), 1826, 1924.
1909a. Siebenrock, 594.
1910. Müller, L., 624.
1910. Sternfeld, 8.
1912b. Werner, 493.
1913. Siebenrock, 43, fig. 22.
1917. Sternfeld, 416.
1919. Schmidt, 601.
1924a. Werner, 269.
1925. Flower, 935.
1929. Flower, 54.
1934a. Mertens and Müller *in* Rust, 12.
1937. Andersson, 3.
1937a. Flower, 16.

Further citations of "*senegalensis*" and "*baikii* (part)" will be found under *Cyclanorbis elegans*.

Common names. Senegal Soft-shelled Turtle (Flower:1929); African Bungoma (Gray:1844).

Illustrations. Dorsal, ventral and lateral views of the shell are furnished by Gray (1855:pl.xxix), also the skull and jaws

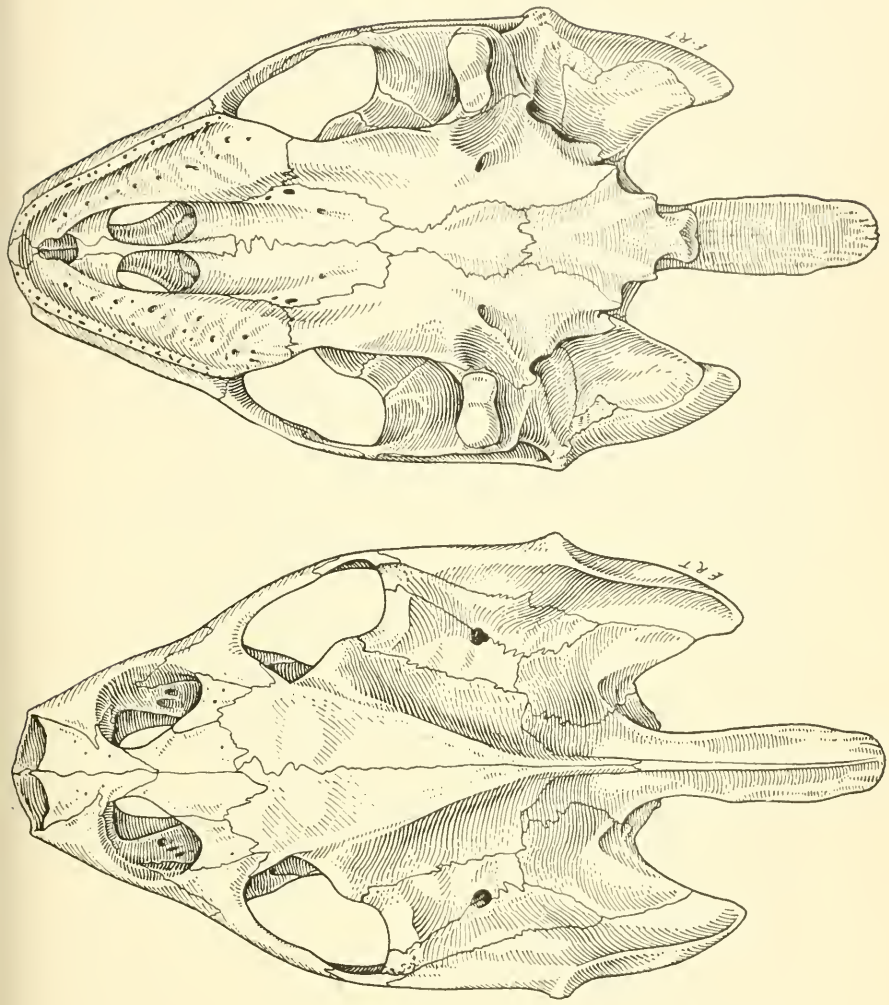


Fig. 57. Skull of *Cyclanorbis senegalensis* (B.M. 65.5.9.20), x ⅓. Dorsal and ventral views.

(E. R. Turlington del.)

(Gray:1864c:figs.16-18), while Siebenrock supplies dorsal (1913b:fig.22) and ventral (1902b:fig.16) views of the plastron.

Description of hatchlings and young.[1] Proboscis projecting, the distance from its tip to the orbit (not eye) shorter than, subequal to, or greater than the orbital diameter; nostril with papilla-like process projecting upwards from its infra-median corner; upper lips meeting in front to form a flat arch; forefoot with 5 or 6, sharp-edged, crescentic skinfolds on its upper surface (see Fig. 51*C*), another indistinct weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary, not projecting beyond the posterior rim of the carapace.

Carapace of young with a moderate vertebral keel and numerous, raised, rather wavy, longitudinal lines comprised of small individual tubercles anteriorly converging toward a strongly tubercular nuchal area, leathery margin posteriorly smooth, not extensive, scarcely extending beyond the tail.

Plastron of young, smooth, without callosities; femoral and caudal flaps permit concealment of hind limbs and (probably) tail.

Osteological description. Skull. Distance between tip of premaxilla and orbit greater than the long diameter of orbit; height of orbit about twice the interorbital width, which is less than the width of naris; premaxilla single, not separating maxillae underneath the naris; inward extensions of the maxillary triturating surfaces anteriorly narrowing the small intermaxillary foramen, almost excluding the premaxillae from its medio-anterior margin, elsewhere bordering the foramen (except sometimes mediposteriorly where the maxillae may be separated by the vomer, which then also separates them behind the foramen); length of the foramen subequal to its distance from the anterior choanal margins; vomer slender, without ascending processes to prefrontals; its interchoanal portion moderately long; choanae bordered by the triturating surfaces, postorbital arch about equal to half the long diameter of the orbit; orbit broadly entered by jugal, which is in contact with the parietal; squamosal crests short and blunt; pterygoids meeting opisthotic, greatly restricting postotic fenes-

[1] Based on two Maccarthy Id. hatchlings (B.M. 1901.7.16.26-27), a hatchling and two young from Togo (in the Berlin Museum), and seven specimens from the Schari River near Fort Archambault, French West Africa.

tra; mandible without symphysial ridge, its symphysial width less than the long diameter of the orbit.

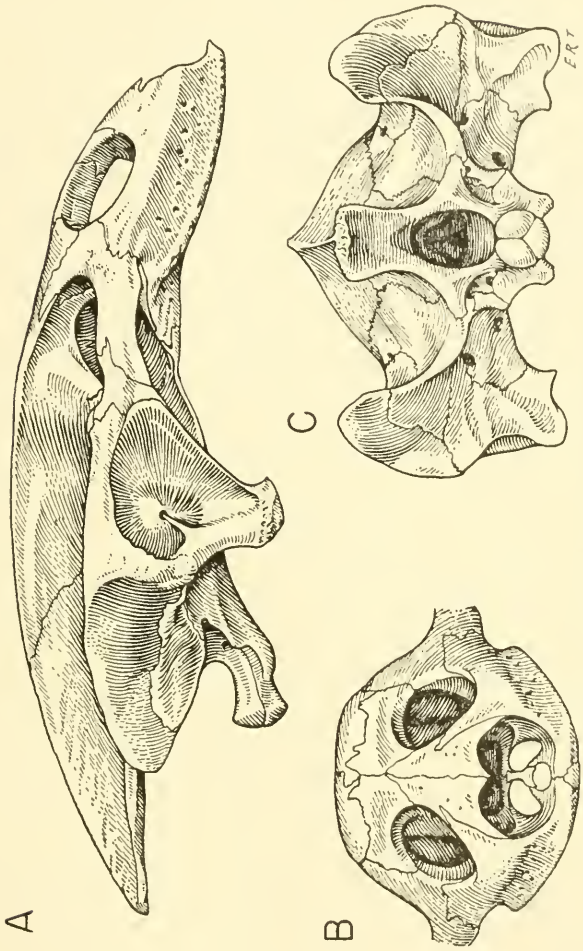


Fig. 58. Skull of *Cyclanorbis senegalensis* (B.M. 65.5.9.20), × $\frac{1}{3}$. *A*, lateral view; *B*, anterior view; *C*, posterior view.

(E. R. Turlington del.)

Carapace. Carapacial bones rather finely granulated and vermiculated; a prenuchal bone in adults; nuchal bone not notched laterally, extending slightly below the first pleurals, between which are two neurals; neurals variable in number, not forming a continuous series; pleurals 8 pairs, a variable number in contact medially.

Plastron. Preplastra widely separated, the anterior branch longer than the posterior; epiplastra fused, forming an acute angle, their pointed posterior prong inserted in a deep notch which separates the rounded inner margin from the strongly convex anterior border of the fused hyo- and hypoplastra; posterior border of this compound bone very deeply excavated, the anteromedial process with several almost juxtaposed prongs, the medial process very short, scarcely projecting beyond the rim, the posteromedial process with only 3 prongs between which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra oblong, slightly wider at their anterior and posterior ends, with 1 or 2 notches posteriorly, converging posteriorly but nowhere in contact.

Callosities 7 to 9, sculptured like the carapace, extremely developed in adults except on the xiphiplastra where they may be absent, even in adults; regularly present anteriorly, but not overlying any bones, are two small, subquadrilateral callosities in contact medially; posteriorly these are in contact with the preplastral callosities, which are large oblique ovals in contact medially; fitting between the latter posteriorly is the forwardly directed apex of the fused epiplastra bearing a large triangular callosity; in this general anterior region additional callosities are sometimes present (*fide* Gray:1865d); hyo-hypoplastral callosities, covering almost the entire surfaces of these bones, nearly meet medially; xiphiplastral callosities poorly developed or absent.

Pointing out that the callosities increase in number and size with age, but that their development appears to proceed more slowly in the Nile than in West African rivers, Siebenrock (1906) states that the hypoplastral callosity changes in shape as it develops. This is borne out by the B.M. and Vienna material examined by E.E.W.

Thus while fully adult *senegalensis* have the hyo-hypoplastral

callosity strongly convex anteriorly, as described above, in younger specimens the anterior edge of this element is straight — as in adult *elegans*. From the Schari River series in Vienna Museum it would appear that the anterior convexity occurs in specimens with a carapace length between 210 and 220 mm. But while the anterior convexity of the hyo-hypoplastral callosity is not developed in *senegalensis* with carapace lengths of 200 mm. or under, there is a greater development of all the callosities in all *senegalensis* (except hatchlings and near hatchlings) than there is in *elegans*. Thus, while callosities are already well indicated on a Schari River *senegalensis* with a carapace length of 128 mm., there is still no trace of them on a Schari River *elegans* of 170 mm.

In Schari River *senegalensis* the first traces of preplastral callosities appear in specimens with a carapace length of 128 mm., and these have become quite large in those with a carapace length approaching or exceeding 200 mm. In *elegans*, so far as is known, preplastral callosities are never developed. This fact, together with the more retarded condition of the hyo-hypoplastral callosity in *elegans* as compared with *senegalensis* of the same size, and differences in coloration, should always permit separation of young *elegans* from halfgrown *senegalensis*.

Color. Carapace of hatchling grayish or brownish, sparsely punctate with black and indistinctly mottled with lighter, most clearly around the posterior periphery which may be edged with lighter. Plastron yellowish or cream colored, centrally quite heavily blotched with darker. Head, neck and limbs gray or brownish, finely spotted with white or indistinctly vermiculate with lighter; throat, and neck below, whitish (based on five specimens seen by us, viz. three hatchlings from Macarthy Id. and Togo, also two young from Togo).

Carapace of adult blackish olive, the periphery narrowly edged with white; plastron pure white or yellowish, clouded with brown. Head above, olive or blackish, sparsely punctate with lighter, sides of head indistinctly vermiculated with dusky (Gray:1870d:pl. xliii, not text).

Carapace of adult light brown, its fleshy margin dark brown, immaculate. Plastron yellow. Head and neck above, olive green; below, yellow (*fide* Siebenrock:1905a).

Size. Length of dorsal disk of a hatchling (Berlin Mus. 26687) from Kundja Konkomba, Togo, *ca.* 46 mm.; of a gravid ♀ from Duem, 225 mm. (Siebenrock:1906a); length of largest disk, 350 mm. (Boulenger:1889a).

Breeding. On April 12th, at Duem, 6 hard-shelled, almost spherical eggs measuring 36 mm. in diameter, were removed from a ♀ whose cloaca was so flaccid that Werner thought she must have been captured while laying (Siebenrock:1906a).

Longevity. Ten years, 2 days, and still living in London Zoo at the time of the report (Flower:1929).

Enemies. These turtles are hunted by the Bari tribesmen of the Bahr el Jebel who utilize the carapacial disks as basins, and esteem the fleshy margins for their food value (Werner; cited by Siebenrock:1906a).

Defense. When these turtles are molested they withdraw their heads and forelimbs, enclosing them by raising the anterior plastral lobe to meet the carapacial margin; the hind limbs are similarly withdrawn beneath the protecting femoral flaps (Sternfeld:1917).

Habits. During the Gambian rainy season young *senegalensis* move into the marshes where four were captured. Africans place these turtles in their wells, possibly to keep them free of putrifying matter as Anderson (1937) suggests.

Localities. Sudan: Bahr el Zeraf; White Nile at Duem, and north to Renk, and at Tonga. *French Equatorial Africa:* *Gabon (skull in M.C.Z.); *Schari River near Fort Archambault (V.M.). *French Cameroon:* Lake Tchad (also as Chad and Tsade). *Togo:* Kundja Konkomba; Mango (Mangu). *Nigeria:* Lagos; Niger River at Lohata, Kabba Province. *Gambia:* Gambia River; Maccarthy Island. *Senegal:* (Type locality).

Range. Sudan west through French Cameroon and Gabon to Senegal.

"Cyclanorbis" sp.

By the courtesy of Dr. Eiselt of the Naturhistorisches Museum, Vienna, we have been able to examine the soft-shell-turtle hatchling said by Werner (1924a:270) to have come from the northwest shore of Lake Tanganyika. This specimen, as noted on p. 420, will not key out even generically on the characters

used by us. In having the distance from tip of the proboscis to the orbit greater than the orbital diameter (in so young a specimen), it resembles *Cyclanorbis* rather than *Cycloderma*. In possessing a caudal flap as well as femoral flaps it resembles *Cyclanorbis senegalensis* or the species of *Cycloderma*. In coloration, being without spots or vermiculations on head, neck, carapace or plastron, it differs from all other African soft-shells examined by us. This hatchling may be a local variant of *senegalensis,* but at present no soft-shell turtle is known from Lake Tanganyika. It may well represent a new form, but we consider it undesirable to erect a new name on the basis of a single hatchling of somewhat indefinite origin.

Description of hatchling (V.M. 14826) from northwest shore of Lake Tanganyika. Proboscis projecting, the distance from its tip to the orbit greater than orbital diameter; nostril with papilla-like process projecting upwards from the inframedian corner; forefoot with 4, sharp-edged, crescentic skinfolds on its upper surface, another indistinct weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary, not projecting beyond the posterior rim of the carapace.

Carapace with a moderate vertebral keel and numerous raised, wavy, longitudinal lines comprised of small tubercles anteriorly converging toward a tubercular nuchal area; leathery margin posteriorly smooth, not extensive, scarcely extending beyond the tail.

Plastron smooth, without callosities; femoral and caudal flaps permit concealment of hind limbs and (probably) of tail.

Color. Carapace uniform olive (olive-green *fide* Werner). Plastron uniform yellowish white. Head and neck above, gray-brown (gray-green: Werner) without spots, lines or vermiculations; throat and neck below, yellowish white.

Size. Length of dorsal disk (V.M. 14826) 70 mm.; breadth 60 mm. (as given by Werner).

Genus CYCLODERMA Peters

1854a. *Cycloderma* Peters, Monatsb. Akad. Wiss. Berlin, p. 216. Type: *Cycloderma frenatum* Peters.

1859. *Heptathyra* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 294. Type: *Cryptopus aubryi* A. Duméril.

1856. *Cryptopodus* Duméril, Revue Mag. Zool. (2), 8, p. 374. Lapsus for *Cryptopus* Duméril and Bibron, 1835.

1860a. *Aspidochelys* Gray, Proc. Zool. Soc. London, p. 6. Type: *A. livingstonii* Gray = *frenatum* Peters.

Definition. Cutaneous femoral flaps present, permitting concealment of the hind limbs.

Skull without maxillary ridging; intermaxillary foramen small; postfrontals not meeting vomer; jugal broadly in contact with parietal; postorbital arch wider than diameter or orbit; pterygoids joining opisthotic, greatly restricting fenestra postotica.

Carapace without prenuchal bone, without peripheral ossifications; nuchal bone notched laterally, ventrally with raised posterolateral processes which tend to underlie the first pleurals, between which are two neurals, rarely one; neurals 8 or 9, rarely 7, pleurals 8 pairs, the seventh and eighth, or eighth only, in contact medially.

Plastron with preplastra short and straight; hyo- and hypoplastra fused, their posteromedial process with three prongs between which are inserted the two anterior prongs of the adjacent xiphiplastron; callosities in adults 7, always present on gulars.

Range. East (Tanganyika Territory south to Mozambique) and West (Portuguese, Belgian and French Congo) Africa.

Fossil record. First reported in the Lower Miocene of Kenya; also known from the Pleistocene of Lake Rudolf. Although these remains are certainly cyclanorbide, the generic identification is uncertain; they may be referable to *Cyclanorbis*.

Remarks. The unity of the genus *Cycloderma* is clearer than that of *Cyclanorbis*. Discrimination of the two species is also very easy. There is, however, the possibility of a taxonomic problem within the species *frenatum*. The original Zambezi series were described by Peters as being dark green in general color, as also shown on his plate. Our material[1] from Lake Nyasa and the Ruvuma River, however, consists of pale gray to leaden hatchlings and pale to dark olive adults. Other minor differences are noted in the color description below (p. 464).

[1] Twenty-one juveniles and 11 adults (Loveridge coll.).

There may be also a parallel osteological difference. The skulls[1] of all our *frenatum* from Lake Nyasa and the Ruvuma lack a vomer, for which, in fact, there is no evident place of attachment. On the other hand, a vomer, though very narrow and much reduced, is shown in Peters' figure of a Zambezi skull. The vomer is present in a Zambezi specimen (B.M.) as well as another skull (Senck. Mus.), unfortunately without locality, seen by one of us (E. E. W.).

Thus the possibility of constant color and skull differences between the nominate population of the Zambezi, and those from further north needs to be investigated. Should these differences hold good, the more northerly populations will merit subspecific distinction.

No suspicion of geographical differentiation attaches to *aubryi*, but in this case there is an interesting biological problem. The pattern of *aubryi* is very distinctive, indeed unique among trionychids. On the head and nape is a chocolate brown vertebral streak which is continued on to at least the anterior third of the rather light brownish disk. Curiously enough, in the same West African rain-forest region inhabited by *C. aubryi*, a very similar pattern is present in two species of the pleurodiran genus *Pelusios*. The juveniles of both *P. gabonensis* and *niger* have similarly light brown carapaces with a black vetebral stripe which, in *gabonensis*, is continued on to the head. While in *C. aubryi* the pattern persists throughout life, in *P. niger* it occurs only in the hatchling stage, and has an intermediate duration in *P. gabonensis*. The significance of this apparent mimicry is quite unknown.

Cycloderma aubryi (Duméril)

1856a. *Cryptopodus Aubryi* Duméril, Revue Mag. Zool., (2), **8**, p. 374, pl. xx: Gabon, French Congo.
1859. *Heptathyra aubryi* Cope, 294.
1864c. Gray (part), 93, figs.
1870e. Gray, 93.
1884a. Rochebrune (in error), 28, pl. ii, figs. 1-2.
1860. *Cycloderma aubryi* Duméril, 166.
1875a. Peters, 196.
1876a. Peters, 117, pl. —, figs. 1-2.

[1] Seven skulls (Loveridge coll.).

1877c. Peters, 611.
1880b. Vaillant, 797.
1880c. Vaillant, 53, pl. xxx, fig. 13.
1889a. Boulenger, 267.
1895a. Bocage, 8.
1896. Günther, 263.
1897. Sjöstedt, 33.
1898a. Werner, 204.
1900b. Boulenger, 447.
1902b. Siebenrock, 836, fig. 14.
1902c. Tornier, 665.
1906i. Boulenger, 197.
1906a. Mocquard, 480.
1909a. Siebenrock, 593.
1910. Sternfeld, 8, fig. 15.
1917. Sternfeld, 415.
1919. Schmidt, 598.
1929. Flower, 53.
1933m. Witte, 68.
1934a. Mertens and Müller *in* Rust, 12.
1950. Williams, 552.
1953a. Laurent, R., 21, 26.
1953. Witte, 21.
1864c. *Heptathyra frenata* Gray (part), 94.
1873b. Gray (part), 76.

Common name. Aubry's Soft-shelled Turtle (Flower:1929).

Illustrations. The black and white drawings on plate xx of Duméril's original description (1856a), copied here as our Plate 18 (top), clearly show the principal characteristics.

Description. Proboscis projecting, the distance from its tip to the orbit (not eye) shorter than or subequal to (in young), or longer than (in adults), the orbital diameter; nostril without papilla-like process projecting from its infra-median corner; upper lips meeting in front to form a more or less pointed arch; forefoot with 6 or 7 sharp-edged, crescentic skin-folds on its upper surface, another weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary,[1] not projecting beyond the posterior leathery rim of the carapace.

Carapace of young with a moderate vertebral keel and numerous tubercles, those in center not arranged in longitudinal lines,

[1] Possibly slightly longer in ♂♂ than in ♀♀.

the lateral ones showing a tendency to such arrangement; carapace of adults smooth in life, at least centrally, but showing, when dried, the underlying bony sculpture; the disk with a distinct nuchal excavation, less convex, shorter and rounder than in *frenatum;* leathery margin not extensive, posteriorly scarcely extending beyond tail.

Plastron of hatchlings smooth, without callosities; in young (90 mm., M.C.Z. 4300) callosities present on preplastra, *on the fused epiplastra,* hyo-hypoplastra and xiphiplastra; at this age the anterior edges of the hyo-hypoplastral callosities are almost straight, later becoming strongly convex anterolaterally; in adults the azygous callosity is subcircular, large; hyo-hypoplastral callosities in contact with xiphiplastral callosities by long straight sutures; femoral and caudal flaps permit concealment of hind limbs and tail.

Osteological description.[1] Skull. Distance between tip of premaxilla and orbit greater than long diameter of orbit; height of orbit about one-third greater than the interorbital width, which is somewhat less than the width of naris; premaxilla apparently absent; intermaxillary foramen small, pear-shaped with apex directed forwards; both in front and behind this foramen the maxillae in contact medially, the posterior medial suture much longer than the foramen; vomer slender without ascending processes to prefrontals, its interchoanal portion relatively elongate; choanae restricted anteriorly by inward expansion of the triturating surfaces, expanding abruptly posteriorly; postorbital arch much wider than the long diameter of orbit; orbit not entered by jugal, which is excluded by broad contact of postorbital and maxilla but is broadly in contact with parietal; squamosal crests long, sharp, incurved; pterygoids meeting opisthotic, greatly restricting postotic fenestra; mandible without symphysial ridge, its ventral symphysial width much less than diameter of orbit.

Carapace. Carapacial bones finely granulated and vermiculated; no prenuchal bone; nuchal bone notched laterally, underlying the first pleurals, between which are two neurals; neurals 8 or 9, forming a continuous series; pleurals 8 pairs, the eighth in contact medially.

Plastron. Preplastra (no information); epiplastra fused, forming an obtuse angle, their pointed posterior prong inserted

[1] Based on B.M. 63.6.13.5 only.

in a deep notch which separates the rounded inner margin from the strongly convex outer margin of the fused hyo- and hypoplastra; the posterior border of this compound bone very deeply excavated, its anteromedial process with 2-3 juxtaposed prongs.

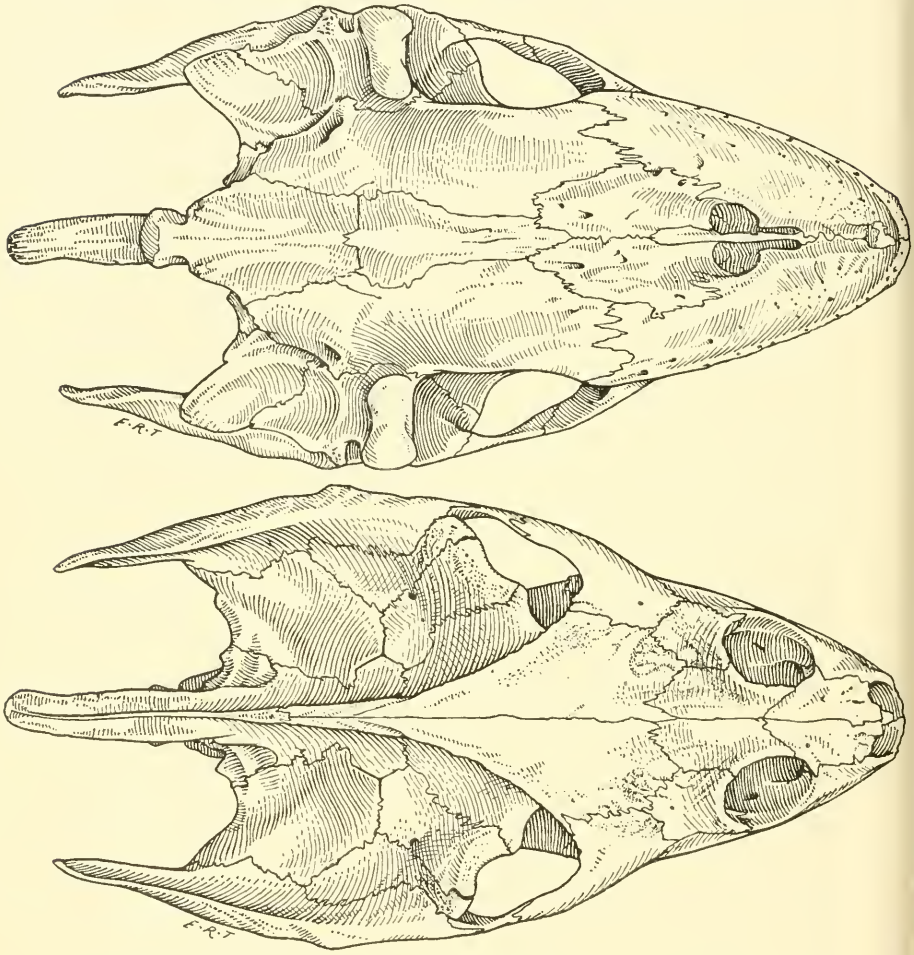


Fig. 59. Skull of *Cycloderma aubryi* (B.M. 63.6.13.5), x ⅝. Dorsal and ventral views.

(E. R. Turlington del.)

the medial process very short, *not* projecting beyond the rim, the posteromedial process with 3-4 prongs, between the lateral three of which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra rather wide with 3 prongs posteriorly, in contact medially by a prong of one fitting into a notch on the other.

Callosities 7, sculptured like the carapace, extremely developed in adults, covering most of the plastral area; preplastral callosities large, nearly half-moon-shaped, in contact medially by a long straight suture; fused epiplastra bearing a large, almost round, azygous callosity; hyo-hypoplastral callosities large, covering most of the surfaces of these bones and almost meeting medially, meeting in an oblique straight line the large trapezoidal xiphiplastral callosity; xiphiplastral callosities in contact medially over their entire length.

Color. Carapace of young dull orange to yellow brown with a few scattered brown or black specks or blotches and a chocolate brown line on the anterior third of the vertebral keel.

Plastron mostly yellow, anteriorly a broad chocolate brown, more or less V-shaped marking whose truncate arms are directed posteriorly; from the axillae the arms of another, but much larger, black, V-shaped figure converge posteriorly to cover the femoral and caudal flaps; under aspect of the fleshy margin yellow.

Head above, yellow brown with five almost hairlike (sometimes converging anteriorly) longitudinal lines, a median one beginning on the crown extends down the neck (in line with the one on the carapace), two arise in the interocular region and terminate on the occiput, each of the remaining pair commence at the nostril and, passing through the eye, continue along the side of the neck; chin and throat whitish indistinctly flecked with darker; limbs largely dark chocolate brown, each bearing a large yellow patch.

Size. Carapace length *over curve* of the Gabon type, 455 mm., the disk alone *over curve* 330 mm., its breadth 310 mm. (*fide* Duméril:1856a); head and neck together 280 mm. A. Fernan Vaz turtle with head and neck of exactly the same length (11″) is said by Cope (1859) to have a total length of 760 mm. (2′ 6″). Carapace length of an Eala specimen (M.C.Z. 43000) is 90 mm., breadth 80 mm.; both measurements being taken in a straight

line. Carapace length of a Lake "Ogemwe" (? Azinguo) hatchling (B.M. 1908.5.25.3), 55 mm., breadth 44 mm.

Habitat. Included in the rain forest fauna by Schmidt (1919).

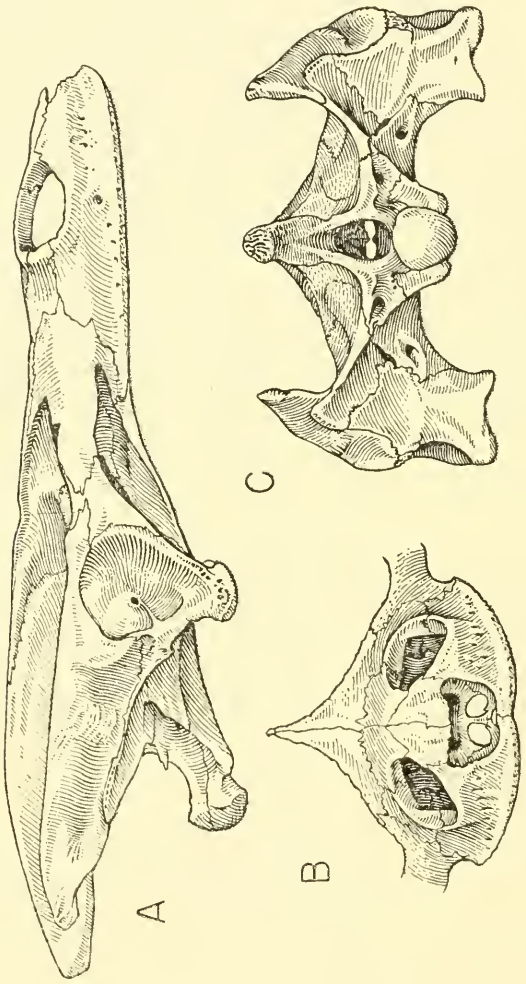


Fig. 60. Skull of *Cyclodermα aubryi* (B.M. 63.6.13.5), x $\frac{5}{6}$. A, Lateral view; B, anterior view; C, posterior view. (E. R. Turlington del.)

Localities. Cabinda: Chinchoxo. *Belgian Congo:* *Eala, Flandria, (i.e. Bokele), Equateur Province; *Tumba, Lake Loondo (B.M.). We concur with de Witte (1953) that the "Katanga: 1898" specimen is a very questionable record. *French Equatorial Africa:* Fernan Vaz (Fernando Vas); Gabon; *Lake "Ogemwe" (B.M.) (?Azinguo); Lambarene (Limbareni); Ogoue (Ogowai); Oubangui (Ubangi) River near Libengue (Libenge).

We know of no specimen actually taken in the Cameroons. Its alleged presence there dates from a list by Sjöstedt (1897) who failed to collect it. Subsequently cited in the lists of Werner (1898a) and Sternfeld (1910), but without material.

Range. Portuguese, Belgian (western) and French Congo.

Cycloderma frenatum Peters

1854a. *Cycloderma frenatum* Peters, Monatsb. Akad. Wiss. Berlin, p. 216: Zambezi River, Mozambique.
1882a. Peters, 14, pls. i-iiia.
1889a. Boulenger, 265.
1894a. Günther (1893), 618.
1896a. Bocage, 97.
1897. Johnston (also 1898 ed.), 356, 361.
1900b. Tornier, 583.
1902b. Siebenrock, 834, fig. 13.
1902b. Tornier, 580.
1909a. Siebenrock, 592.
1913c. Nieden, 64.
1929. Lindholm, 291.
1934a. Mertens and Müller *in* Rust, 12.
1934. Pitman, 307.
1937f. Loveridge, 489, 495.
1942e. Loveridge, 251.
1946. Mitchell, 21.
1950. Rose, 330, figs. 198-199.
1950. Williams, 552.
1953c. Loveridge, 160.
1855. *Cyclanosteus frenatus* Gray, 64 (ex Peters MS).
1860a. *Aspidochelys livingstonii* Gray, Proc. Zool. Soc. London, p. 6, pl. xxii, figs. 1-2: Tributaries of the Zambezi River, Mozambique.
1860f. Gray, p. 430.
1864c. *Heptathyra livingstonii* Gray, 94.
1864c. *Heptathyra frenata* Gray (part), 94.

1870e. Gray, 93.
1873b. Gray (part), 76.
1884a. Rochebrune (in error), 30.

Synonymy. Further citations of "*frenata*" will be found under *Cycloderma aubryi*, with which this species was confused by Gray (1864c). *Aspidochelys livingstonii* was supposed to be generically distinct because of certain characters of the callosities; when Gray realized these developed with age he himself (1870e) synonymized *livingstonii* with *frenatum*.

Common names. Zambezi Soft-shelled Turtle (English); Zambezi Mud-Turtle (Loveridge); "*cassi* or *ncassi*" (at Sena and Tete: Peters, but see below); *kalibungu* (Sena: Mitchell); *litetamera* (Yao: Loveridge); *mbulundwe* (Yao: Mitchell); *nahi* (Makonde: Loveridge); *nkhasi* (Manganja and Cewa: Mitchell).

Illustrations. Peters (1882a) furnishes fine colored drawings (pl. i, copied as our black and white Plate 18 [bottom]), of dorsal and ventral aspects of what is presumably a ♂; also a figure (pl. iiia) showing plastral marbling in the ♀; skulls, skeleton, etc. (pls. ii-iii).

Description. Proboscis projecting, the distance from its tip to the orbit equal to (in young), or longer than (in adults) the orbital diameter; nostril with papilla-like process projecting upwards from its inframedian corner; upper lips meeting in front to form a flat arch; forefoot with 4 or 5 sharp-edged, crescentic skin-folds on its upper surface, another weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary,[1] not projecting beyond the posterior leathery rim of the carapace.

Carapace of young with a moderate vertebral keel and numerous, raised, rather wavy, longitudinal lines; carapace of adults smooth in life, at least centrally, but showing, when dried, the underlying bony sculpture; the disk is less excavated anteriorly than in *aubryi*, besides being more convex, longer and narrower; leathery margin not extensive posteriorly, scarcely extending beyond tail.

Plastron of hatchling smooth, without callosities (in the young these first appear as small pairs on the preplastra, hyo-hypoplastra and xiphiplastra, while the last to develop is the azygous

[1] Cf. *Sexual dimorphism* below.

element on the fused epiplastra); femoral and caudal flaps permit concealment of hind limbs and tail.

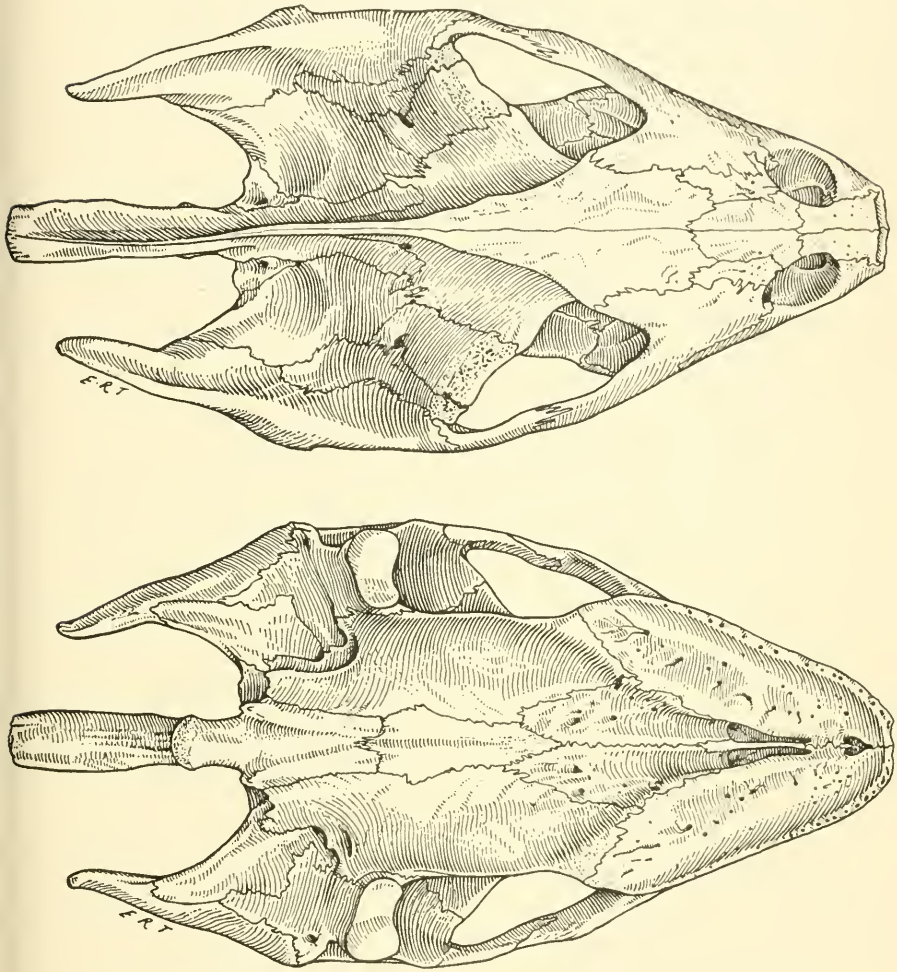


Fig. 61. Skull of *Cycloderma frenatum* (B.M. 84.2.4.1), (Zambezi specimen), x ⅔. Dorsal and ventral views.

(E. R. Turlington del.)

Osteological description. Skull of adult.[1] Distance between tip of premaxilla and orbit subequal to long diameter of orbit; height of orbit about twice the interorbital width, which is less than the width of naris; premaxilla apparently absent (rudimentary, *fide* Peters in Zambezi specimens); intermaxillary foramen small, heart- or pear-shaped with apex directed forwards; both in front and behind this foramen the maxillae in contact medially, the posterior medial suture longer than the foramen; vomer very slender, without ascending processes to the prefrontals, its interchoanal portion relatively elongate, or vomer absent; internal choanae narrowed anteriorly by inward expansion of the triturating surfaces, expanding gradually posteriorly; postorbital arch much wider than the long diameter of orbit; orbit entered by jugal, which is broadly in contact with parietal; squamosal crests long, sharp, incurved; pterygoids meeting opisthotic, greatly restricting postotic fenestra; mandible without symphysial ridge, its symphysial width less than the long diameter of the orbit.

Carapace. Carapacial bones finely granulated and vermiculated; no prenuchal bone; nuchal bone notched laterally, underlying the first pleurals, between which are two neurals, rarely one;[2] neurals 8 or 9, rarely 7,[2] usually forming a continuous series; pleurals 8 pairs, the seventh and eighth, or eighth only in contact medially.

Plastron. Preplastra widely separated, only the anterior branch present; epiplastra fused, forming an acute angle, their pointed posterior prong inserted in a notch which separates the rounded inner margin from the strongly convex anterior border of the fused hyo- and hypoplastra; posterior border of this compound bone very deeply excavated; the anteromedial process with 3 prongs, the medial process typically very short and, as a rule, scarcely projecting beyond the rim; the posteromedial process with only 3 prongs between which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra short and

[1] The skull, with condylobasal length of 31 mm., of a juvenile skeleton (A.M.N.H. 56479) from Lake Nyasa, Nyasaland, shows striking differences in the proportions to those of the adults described above. For example, the distance between tip of premaxilla and orbit is very much *shorter* than the long diameter of the orbit. Presumably similar discrepancies due to ontogenetic change would have been noticed in other African trionychids had skeletal preparations of their young been available.

[2] One only between the first pair of pleurals, and only 7 neurals in one (M.C.Z. 48032) of a series of seven from the Rovuma River.

broad with 3 or 4 notches posteriorly, on the posterior half of each notch a short process joining a similar process on the other element.

Callosities 7, sculptured like the carapace, very well developed

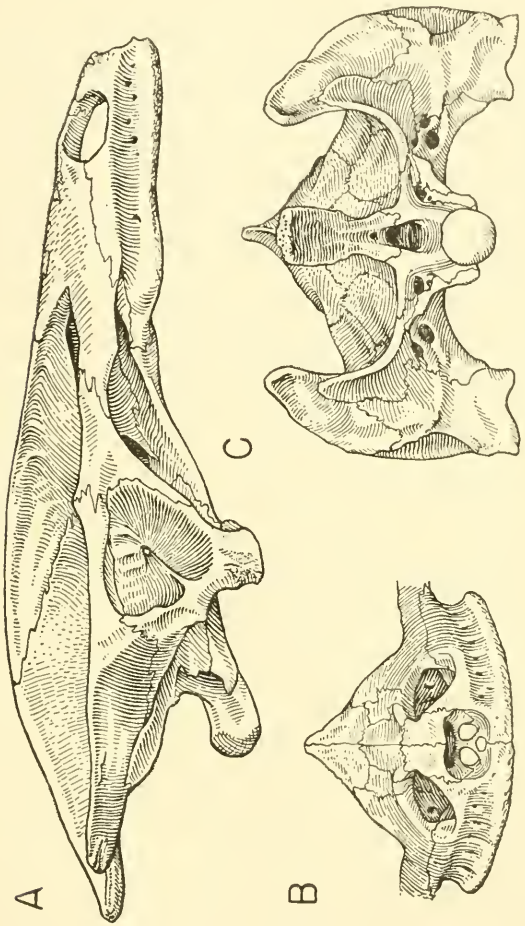


Fig. 62. Skull of *Cycloderma frenatum* (B.M. 84.2.4.1), (Zambezi specimen), x ⅔. *A*, Lateral view; *B*, anterior view; *C*, posterior view.
(E. R. Turlington del.)

in adults; preplastral callosities large oblique ovals, in contact medially; fused epiplastra bearing a small, crescentic to semilunar callosity, smallest of any and last to develop; hyo-hypoplastral callosities covering most of the surfaces of these bones but widely separated medially; hyo-hypoplastral callosities separated from, or in contact with the xiphiplastral callosities by only a short suture; xiphiplastral callosities large oblique ovals, in contact medially.

Color. Carapace in Lake Nyasa hatchlings ranges from pale green to leaden, the periphery usually edged with white; carapace of adults pale to dark olive, uniform or with a trace of blotching. Zambezi turtles would appear to differ somewhat, for Peters (1882a) describes young specimens as green and adults as dark green, uniform, or with interrupted black bands and scattered white spots.

Plastron of Lake Nyasa hatchlings was often almost white, more usually an irregular black blotch was present in the umbilical region, an elongate, oblique blotch near each forelimb, a rounder one anterior to each hind limb, and a smaller sixth spot in the anal region. Plastron of adult ♀ ♀ is china white to flesh-pink almost obscured by pearly gray reticulations. These reticulations are sometimes absent in what may be ♂ ♂. For example, the subject of Peters' colored plate (1882a, pl. i), possibly a Zambezi ♂, is shown as having a cream-colored plastron extensively infuscated with dusky blotches.

The head and neck in Lake Nyasa hatchlings were gray with a dark, light-edged, interorbital crossbar, five similar, but wavy and sometimes broken, longitudinal lines from near occiput to base of the long neck; throat and underside of neck pure white, uniform or showing some dusky streaks. Head and neck of adults very dark olive, the dark longitudinal lines of the young turtle obsolete or, more usually, absent. Peters (1882a), writing of Zambezi turtles, states that the head and neck in both age groups display numerous white dots. Feet gray above, lighter below.

Size. Carapace length *over curve* of a Zambezi ♂, 560 mm., the disk alone *over curve* 470 mm., its breadth 420 mm. (*fide* Peters:1882a, whose figures do not quite tally, for he gives the total length as 970 mm., though head and neck together are only

340 mm., the tail, which would not project beyond the carapacial margin, 65 mm.).

Overall carapace length (*in a straight line*) of three Nyasa ♀ ♀ averaged about 560 mm., breadth 418 mm. The head and neck of one (M.C.Z. 50357) measures 420 mm.; breadth of head 100 mm. Disk length of largest gravid Rovuma ♀ (M.C.Z. 48030) 390 mm., its width (also without leathery margin) 310 mm. (Loveridge:1942e and 1953e).

Overall carapace lengths of 31 Nyasa hatchlings were from 40 to 48 mm., their breadths 30 to 36 mm. Peters mentions a Zambezi hatchling of 45 mm.

Weight. Weight of largest Zambezi ♂ between 28 to 30 lbs. (as 13-14 kilos., Peters:1882a); that of largest Rovuma ♀, 25 lbs. (Loveridge:1942e).

Sexual dimorphism. Possibly the sexes of adults, though not of young, may be told by the fact that the tail of the ♂ is visible in ventral view (cf. Peters:1882a:pl. i), while that of the ♀ is concealed beneath the caudal flap (*ibid.*, pl. iiia, fig. 1). We are unable to confirm Peters' statement that the carapace is narrower in ♂ ♂ than in ♀ ♀ (the relative proportions said to be 1:1⅓ and 1:1¼) or that the union between carapace and plastron is longer in ♂ ♂ than in ♀ ♀.

Breeding. On January 11th, at Tete, a hatchling with umbilical scar was found by Peters (1882a). Between December 24th and early February, at Fort Johnston, nine hatchlings were taken by B. L. Mitchell (letter of 10.iv.47). On February 7th, at Mtimbuka, natives brought in three clutches of eggs numbering 15, 16 and 19, respectively. On February 10th, 19th and 28th, three ♀ ♀ were captured when coming ashore to lay. All three held spherical, hard-shelled eggs ranging from 33 to 35 mm. in diameter. One ♀ laid 3 eggs before being killed, 19 more were present in her oviducts, and many shell-less ova of various sizes were present in the ovaries. On February 7th, the fourth day after a heavy downpour that terminated about eight months drought (but did not inaugurate the rains as was hoped), a young turtle, its carapace caked in mud, was found. Twenty other hatchlings were collected during the three weeks following (Loveridge:1953e). On March 27th and 28th, at Kitaya, two ♀ ♀ held 17 and 19 hard-shelled eggs ranging from 31 to 32

mm. in diameter; in addition one turtle held 55 small ova in various stages of development. (Loveridge:1942e).

Diet. The powerful, all-pervading, fishy odour of Kitaya turtles led Loveridge (1942e) to suggest that these reptiles subsist largely on fish in the Rovuma River. Mitchell found that captive hatchlings from Lake Nyasa eagerly took fine strips of fish or meat from his fingers. However, he concluded (1946:21) that feral adults subsist principally on aquatic snails and mussels. At Mtimbuka the former were *Lanistes ellipticus* and *L. sordidus;* the clams proved to be *Mutela alata* and *simpsoni*, with a robust cockle-like shell (*Caelatura nyassensis*) particularly abundant (Loveridge:1953e).

These large mussels embed themselves vertically in the mud or sandy bottom of lakes and ponds, and considerable effort is required to dig them out. For the purpose, *Cycloderma* must use the powerful claws on its forefeet. Usually the shells are crushed and swallowed, though occasionally undamaged valves have been defecated by freshly captured turtles (Mitchell: 1946).

Parasites. Leaches were present on turtles at Kitaya and Mtimbuka; two removed from the neck of a Lake Nyasa ♀ (M.C.Z. 50357) were of the family Glossiphonidae, possibly *Placobdella jaegerskioeldi.*

Enemies. In 1926 Dr. J. O. Shircore observed two small rufous otters running around a dessicating puddle about 100 yards from the right bank of the Kilombero River, Mahenge District. The object of their interest appeared to be a soft-shelled turtle that had withdrawn within its defenses. At least this was its position when he reached the spot after shooting one of the otters. Subsequently, Dr. Shircore sent a photo of turtle and otter to one of us (Loveridge:1942e).

On February 11th, 1949, Loveridge saw scores of eggshells on the village middens around Mtimbuka. A Yao, whose home was only about ten miles north of Mtimbuka, accepted turtle eggs gladly, but the more sophisticated members of the staff scorned the idea of eating them. Loveridge, himself, ate 18, finding them quite edible though not as palatable as fowl's eggs. It is when coming ashore to lay that these turtles fall an easy prey to Africans; consequently ♂ ♂ are rare in collections (Loveridge: 1953e).

Defense. Though presumably, when molested, *Cycloderma* is capable of inflicting a severe bite with its strong crushing jaws, instead it withdraws both head and forelimbs within the fleshy margins of its shell, the hind limbs beneath dermal flaps, thus completely closing the plastron before and behind. When picked up, however, a *Cycloderma* is occasionally difficult to handle, for vigorous kicking of the clawed feet, which can reach any part of the shell's edge, may displace the captor's hands (Mitchell: 1946).

Temperament. In stating that *Cycloderma* "are very fierce," Johnston (1897) was apparently attributing to them the well-merited reputation of *Trionyx.* Actually these turtles are timid and inoffensive, withdrawing their heads and limbs within the protection of the shell at the slightest disturbance. When all is quiet, the head is protruded with the utmost caution by very gradual stages and withdrawn precipitately to the accompaniment of a kind of snort at the least sound or movement in their vicinity (Loveridge:1942e:252, which consult for a concrete example of such timidity). This inoffensiveness is confirmed by Mitchell (1946).

Habits. Surprisingly active according to Peters (1882a), both in the water and on land where, using their forefeet and snout, they quickly burrow into soft mud in an effort to hide. One of these turtles, with head held well above the surface, paddled swiftly past Loveridge (1942e) as he was wading thigh-deep in a lake. When twenty feet away the reptile dived and was seen no more.

Mitchell (1946) states that during the daytime two captive turtles, that he kept in a pond at Salima, remained for long periods with their nostrils protruding from the water. They did not rise to the surface between 4.00 P.M. and 8.30 A.M. and remained on the bottom during cold weather. He suggests that at such times they obtain oxygen by means of the mass of blood vessels on the unpigmented ventral surface in the vicinity of the flaps. Their only attempts at escape were made at night during rainy weather, or after the water in their pond had been changed. One turtle that got away was recaptured a fortnight later; though without water during this time the reptile was apparently none the worse.

In January, when Loveridge (1953e) endeavoured to secure topotypic *frenatum* near Tete, local native fishermen asserted that these turtles would not be seen until the rains, already two months overdue, broke.

Habitat. Rivers, lakes and stagnant ponds.

Localities. Tanganyika Territory: Kilombero River, Mahenge District (sight record by Shircore; photo seen by A.L.); Lake Nyasa at Manda (as Wiedhafen); *Rovuma River at Kitaya. *Mozambique:* Lake Inhalutanda near Tete; Licuare River, tributary of the Zambezi; *Zambezi River near Tete. *Nyasaland.* *Chowe; *Lake Nyasa at Mtimbuka and at Fort Johnston[1]; Lake Shirwa (Chilwa) ("said to occur": Mitchell); Upper Shire; Lower Shire ("said to occur, but rare": Mitchell). ?*Northern Rhodesia:* chelonian remains near Munyamadzi River, Luangwa Valley, Mpika District (*fide* Pitman).

The erroneous recording by Tornier (1900b) of Fülleborn's specimen as from "Wiedhafen, Victoria Nyassa," resulted in later authors adding Victoria Nyanza or Lake Victoria to the range.

Range. Southern Tanganyika west and south through Nyasaland and possibly Northern Rhodesia to Mozambique (Zambezi River).

Gray's records (1864c: 1873b) for Gabon were due to confusion with *aubryi.*

MARINE TURTLES

General Remarks

The treatment being given to the marine turtles of the families CHELONIIDAE and DERMOCHELYIDAE, differs substantially from that accorded to the other Cryptodira of Africa. While African to the extent that, without exception, they land on the continent or its offshore islands to deposit their eggs, the group is so cosmopolitan that any revisionary study of them should be undertaken on a worldwide rather than a regional basis. This, lacking adequate material, we have not attempted.

The literature dealing with African records, to which — with

[1] We presume that this is also the correct locality for a British Museum specimen labeled "Zomba." Zomba, where Sir Harry Johnston lived, was presumably only the dispatching point of the donor.

few exceptions — we have restricted our citations, is scanty in the extreme. Though there are good reasons to suppose that turtles are by no means rare in the waters surrounding the African continent, yet for extensive areas there are curious gaps in the record. Such hiatuses are presumably due to the failure of travellers to collect and preserve such admittedly cumbersome reptiles.

In the following account, therefore, we present no figures, no analyses of the species, no fossil history, and relatively little general discussion or comment on habits, as we were averse to drawing on extra-territorial sources.

In conformity with this treatment, and in the absence of the necessary material, we have refrained from discussing the alleged Atlantic and Pacific races of the green turtle, hawksbill, loggerhead and leatherback. In all these instances we have listed only the species name and, following it as synonyms, the putative subspecies. Only in the case of the much more distinct *Lepidochelys* races have we registered a decision. We have omitted, as not germane to our area, the problem of the status of *Chelonia depressa* Garman.

For those who desire more complete discussions of the Recent marine turtles, we recommend Deraniyagala (1939) and Carr (1952). The fossil marine turtles are currently being studied by Dr. Rainer Zangerl, to whose publications those interested must be referred.

Incidence of occurrence of the various species on the Senegal coast has been furnished by Cadenat (1949:17) but the figures also reflect edibility or marketable value, suggesting that selection practiced by local fishermen may have influenced the results.

TABLE 10

Marine turtles caught on the Senegal Coast.

Species	Total Individuals Captured	Incidence
Chelonia mydas	256	86.48%
Eretmochelys imbricata	23	7.77%
Caretta and *Lepidochelys*	10	3.39%
Dermochelys coriacea	7	2.36%

Nomenclature. On several occasions Deraniyagala (e.g. 1943) has asserted, though not formally proposed, that on grounds of priority the names of the loggerhead turtles require to be totally altered from present usage, *Caretta* being the correct name of the forms currently called *Lepidochelys,* and *Thalassochelys* the correct name of those now called *Caretta.* The use of the name *Thalassochelys* would involve little hardship since this name is classic, having been applied to both loggerheads by Boulenger (1889a) in the catalogue that all discreet students of this order still faithfully consult. However, an exchange of names such as would be required by the use of *Caretta* for the olive-green loggerheads, rather than for the red-brown forms, is a perversion of nomenclature to be avoided at almost any cost. We therefore venture to comment upon Deraniyagala's reason for proposing the change. He calls attention to the fact that Linnaeus' species *Testudo caretta* was a composite. He believes that the first unambiguous use of the Linnaean name is that of Schoepff (1792), who presents several figures under this name. From the scalation shown in these figures, Deraniyagala deduces that Schoepff was in effect restricting *Testudo caretta* to the form now known as Kemp's Loggerhead.

However, Schoepff's figures appear in editions both with and without colored plates. There are at the Museum of Comparative Zoology four copies of Schoepff, two without and two with colored plates. In the latter editions, apparently not examined by Deraniyagala, the figures of *Testudo caretta* are colored a very fine red-brown, in shade and texture a splendid representation of the red-brown loggerhead. Thus, accepting Deraniyagala's interpretation of the scalation at face value, the color of these plates seems to demonstrate that Schoepff's concept of *Testudo caretta* was, like that of Linnaeus, a composite one.

We have not concerned ourselves with Deraniyagala's reasoning in other regards, nor have we pursued the matter further. We merely wish to protest against the spirit of antiquarian and wholly bibliographic research which leads to these proposals for name changes. We point out that such researches (e.g. in the case of *Trionyx*) almost invariably lead to confusion and instability, insoluble except by the plenary powers of the International Commission. This is the more certain since antiquarian re-

searches will rarely be complete and thus will leave us for all future time at the mercy of the chance discovery of some rare and (nomenclature apart) worthless book.

We deprecate also the forcing of text or figures of the oldest writers into modern standards of precision. As everyone is aware, the figures of the older naturalists were as often as not composite and (with praiseworthy exceptions) rarely accurate, while not infrequently descriptions are unrecognizable beyond the order. The most exhaustive discussion and analysis of such figures and texts can never carry conviction or produce agreement.

In the present case the Copenhagen rules may prevent in fact, as they certainly prohibit in spirit, the changing of these long-accepted names.

Key to the Marine Turtles Breeding in Africa

1. Upper jaw conspicuously bicuspid at symphysis; upper shell covered with smooth skin (or *small* scales in juveniles) overlying a mosaic of small bones and showing 7 prominent longitudinal ridges; limbs clawless.... *Dermochelys coriacea* (Linnaeus) (p. 499).

   Upper jaw not bicuspid; upper shell covered with large horny shields overlying large bony plates, and ridges 0 to 3; limbs with 1 or 2 claws 2

2. Upper shell with 4 pairs of costal shields of which the foremost pair is never the smallest and is separated from the nuchal shield..... 3

   Upper shell with 5 or more pairs of costal shields of which the foremost pair is the smallest and normally in contact with the nuchal shield.. 4

3. Snout not compressed; 2 prefrontal shields on head; shields of upper shell not overlapping (except in very young turtles); usually a single claw on each limb ....*Chelonia mydas* (Linnaeus) (p. 474)

   Snout compressed; 4 prefrontal shields on head; shields of upper shell strongly overlapping (except in very young or very old turtles); usually 2 claws on each limb ..... *Eretmochelys imbricata* (Linnaeus) (p. 485)

4. Upper shell normally with only 5 pairs of coastal shields; bridge on either side of lower shell with 3 enlarged inframarginal shields without pores; color of adults and young predominantly reddish brown..... *Caretta caretta* (Linnaeus) (p. 490)

   Upper shell normally with 6 to 9 (rarely 4 or 5) pairs of costal shields; bridge on either side of lower shell with 4 enlarged inframarginal shields, each with or without a pore; color of adults predominantly olive, of young olivaceous black ..... *Lepidochelys olivacea olivacea* (Eschscholtz) (p. 495)

Family CHELONIIDAE

1882. *Cheloniidae* Cope, Proc. American Philos. Soc., **22**, p. 143.

Definition. Cryptodirous testudinates adapted to marine life. Horny shields normally present; costal scutes 4 or 5 pairs; marginals, exclusive of the nuchal and supracaudals, 11 or 12 pairs; inframarginal series complete; additional axillary shields also present; plastron with 6 pairs of scutes and one unpaired scute; an intergular commonly present.

Skull without nasal bones; prefrontals always in contact dorsally, always with descending processes that are moderately separated inferiorly; temporal region posteriorly very little emarginate; parietal meeting squamosal; no bones tending to be reduced; quadrate never enclosing stapes; postotic antrum absent; parietals with reduced descending processes; upper jaw with or without ridges on its triturating surfaces; vomer always present, separating palatines; mandible with coronoid bone.

Neck vertebrae with only one biconvex centrum, usually the fourth, typically a plane joint between the sixth and seventh centra, the eighth centrum concave in front, doubly or not; coracoids with their median borders moderately expanded; humerus of a specialized marine type with deltopectoral crest far down the shaft; trochanteric fossa of femur reduced by union of the trochanters; phalanges without condyles; claws 1 or 2.

Carapace heart-shaped, united to plastron only by ligament; neither carapace nor plastron hinged; pleural bones somewhat reduced and often peripheral fenestrae persisting till late in life; nuchal without costiform processes but with a ventral attachment area for the eighth cervical; neural bones hexagonal, short-sided in front, variable in number; pygals 3; plastron never cruciform but with some development of fontanelles; entoplastron always present, more or less lance-shaped.

Range. Tropical, subtropical and — as an occasional visitor — temperate oceans.

Genus CHELONIA Brongniart

1800. *Chelonia* Brongniart[1] (part), Bull. Soc. Philom. Paris, **2**, p. 89.

[1] In 1801 this name was used by Sonnini and Latreille (Hist. Nat. Rept., **1**, p. 22) but they correctly attributed it to Brongniart, whose article we have examined.

"Ce sont les tortues de mer." Type: *Testudo mydas* Linnaeus (designation by Fitzinger: 1843).

1837. *Chelona* Burmeister, Handbuch Naturg., **2**, Abt. Zool., p. 731. Type: *T. mydas* Linnaeus (by monotypy).

1838. *Mydas* Cocteau (not of Fabricius: 1799), Rept. in De la Sagra, Hist. Fis. Pol. Nat. Cuba **4**, p. 22. Type: *T. mydas* Linnaeus (by tautonomy).

1843. *Mydasca* Gervais, Dict. Hist. Nat., **3**, p. 457. Type: *T. mydas* Linnaeus (by monotypy).

1845. *Euchelonia* Tschudi, Fauna Peruana, p. 22. Type: *T. mydas* Linnaeus (by monotypy).

1848. *Megemys* Gistel, Naturg. Thier., p. viii. *Nomen novum* for *Chelonia*.

1858. *Euchelys* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 447. Type: *E. macropus* Girard = *T. mydas* Linnaeus (by monotypy).

1862a. *Chelone* Strauch, Mém. Acad. Imp. Sci. St. Petersbourg, (7), **5**, No. 7, p. 59. Type: *Testudo viridis* Schneider = *T. mydas* Linnaeus (by original designation).

Definition. Head with 1 pair of prefrontal shields; postoculars 3-4; claws 1.

Skull with triturating surface of maxilla ridged, the ridge rising to a dentate projection at suture with the premaxillae; premaxillae in contact with vomer which separates the maxillae; maxilla with vertical ribbing on inner surface of its cutting edge; descending processes of prefrontals in contact with vomer and palatines; a blunt ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view concealed by the extensive secondary palate; pterygoids flat posteriorly; frontal usually entering orbit; crista pretemporalis reduced; mandibular symphysis short; the somewhat serrate labial margin (the horny sheath is sharply serrate) rising to a sharp point at the symphysis; the lingual margin surmounted by a wider blunt ridge rising to a higher point at the symphysis, the two points united by a sharp symphysial ridge.

Carapace with persistent lateral fontanelles; neurals 9-11, usually hexagonal, short-sided in front; peripherals 11 pairs, the tenth pair not in contact with the ribs; nuchal shield not in contact with first costals; costals typically 4 pairs.

Plastron with a large intergular shield; inframarginals 4 pairs, without pores.

Range. Tropical, subtropical and — as an occasional visitor — temperate oceans.

Chelonia mydas (Linnaeus)[1]

1758. *Testudo Mydas* Linnaeus, Syst. Nat., ed. 10, 1, p. 197: Ascension Island.
1802b. Daudin, 10, pl. xvi, fig. 1.
1860. Tristram, 405.
1782. *Testudo* (*macropus*), Walbaum, Chelongr. Schildkröten, p. 112: No locality.
1783. *Testudo Viridis* Schneider, Natur. Schildkröten, p. 299: No locality.
1787. *Testudo japonica* Thunberg, Vetensk. Acad. Handl., **8**, p. 178, pl. vii, fig. 1: Japan.
1788. *La Tortue Franche* Lacépède, Hist. Nat. Quad. ovip. Serpens, 1, p. 54; and *Testudo marina* (seu *vulgaris*) in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Torrid Zone.
1788. *La Tortue écaille-verte* Lacépède, Hist. Nat. Quad. ovip. Serpens, 1, p. 92; and *Testudo viridis-squamosa* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Amazon River, Brazil.
1802b. *Testudo cepediana* Daudin, Hist. Nat. Rept., **2**, p. 50, pl. xvii, fig. 1: No locality.
1812. *Chelonia virgata* (Duméril) Schweigger, Königsberger Arch. Naturwiss. Math., pp. 291, 411: Seas of the Torrid Zone.
1814. Schweigger, 21.
1835. Duméril and Bibron, 541.
1849. Smith, A., App., 2.
1855. Gray, 74.
1873b. Gray, 93.
1820. *Caretta esculenta* Merrem, Vers. Syst. Amphib., p. 18: Atlantic Ocean.
1820. *Caretta nasicornis* Merrem, Vers. Syst. Amphib., p. 18: Ocean near America.
1820. *Caretta Thunbergii* Merrem, Vers. Syst. Amphib., p. 19: Japan.
1829. *Chelonia maculosa* Cuvier, Règne Animal, ed. 2, **2**, p. 13: No locality.
1829. *Chelonia lachrymata* Cuvier, Règne Animal, ed. 2, **2**, p. 13: No locality.
1834. *Chelonia bicarinata* Lesson, in Bélanger, Voy. Indes-Orient., Zool., p. 301: Atlantic Ocean.
1835. *Chelonia Marmorata* Duméril and Bibron, Erpét. Gén., **2**, p. 546, pl. xxiii, fig. 1: Ascension Island.
1844. *Chelonia viridis* Gray, 54.
1855. Gray, 75.

[1] For the most part this bibliography is restricted to synonyms, together with citations dealing with African material. Nomenclatorial changes such as *Chelone, Chelonia, midas* and *mydas* call for careful checking.

1875. Melliss, 99.
1858. *Chelonia formosa* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 456, pl. xxxi, figs. 1-4: Fiji Islands.
1858. *Chelonia tenuis* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 459, pl. xxxi, fig. 8: Honden Island, Paumotu Group, Tahiti and Eimeo; Rosa Island.
1865. *Chelone viridis* Strauch, 141.
1885a. Boettger, 172 (as marine turtle, later identified as *viridis*).
1885. Greeff (1884), 49, footnote.
1888a. Boettger, 174.
1890. Büttikofer, **1**, 302.
1866a. *Chelonia midas* Bocage, 41.
1890. Büttikofer, **1**, 266, 269.
1868. *Chelonia Agassizii* Bocourt, Ann. Sci. Nat. Zool. (Paris), (5), **10**, p. 122: Nagulate River mouth, Guatemala.
1872. *Chelonia mydas* Sowerby and Lear, pls. lix-lx.
1878. Reichenow, p. 92.
1882. Pechuël-Loesche, 277.
1882a. Peters, 18.
1906a. Mocquard, 481.
1909a. Siebenrock, 545.
1912b. Werner, 454.
1929. Flower, 38.
1933. Flower, 750.
1936j. Loveridge, 221.
1937a. Flower, 13.
1937e. Hewitt, 15.
1937f. Loveridge, 488.
1949. Cadenat, 16, figs. 1-3, 10, 14, 15a.
1949. Villiers, 165.
1950. Rose, 327.
1950. Williams, 552.
1873b. *Mydas viridis* Gray, 95.
1884a. Rochebrune, 40.
1880. *Chelonia depressa* Garman (part at least), Bull. Mus. Comp. Zool., **6**, p. 124: East Indies juv. (N. Australian adult may be distinct. Also following Fry (1913), we omit *Natator tessellatus* McCulloch, 1908, from Port Darwin, N. Australia, from the synonymy).
1887. *Chelonia lata* Philippi, Zool. Garten, **28**, p. 84: near Valparaiso, Chile.
1889a. *Chelone mydas* Boulenger, 180.
1890. Büttikofer, **2**, 438, 478.
1893a. Boettger, 12.
1895a. Bocage, 6.

1896a. Bocage, 74, 98.
1896. Lönnberg, 11, 12 (on Linnaeus' type).
1901. Gadow, 381.
1901. Steindachner, 326.
1903a. Bocage, 52.
1903a. Boulenger, 92 (footnote), 96.
1906. Johnston, 819, 833, fig. 311.
1906b. Siebenrock, 39.
1908. Sordelli, 17.
1911d. Sternfeld, 51.
1913. Boettger, 318, 330, 332, 335.
1915. Rawitz, 657, pl. xlviii, figs. 59-61.
1923g. Loveridge, 930, 933.
1924b. Loveridge, 3.
1925b. Flower, 932.
1927. Calabresi, 37.
1938. Cozzolino, 241, graphs.
1947. Irvine, 309.
1955. Cansdale, 95, 104.
1925b. *Chelone virgata* Flower, 932.
1931. *Chelone midas* Ingrams, 429.
1934a. *Chelonia mydas mydas* Mertens and Müller *in* Rust, 10.
1934a. *Chelonia mydas japonica* Mertens and Müller *in* Rust, 10.

Common names. Green Turtle; Edible Turtle (English); *anjwa* or *apuhulu* (Nzima of Gold Coast:Irvine); *apuhuru* (Fante of Gold Coast:Irvine); *assa* (Cape Delgado:Peters); *hala* (Ga of Gold Coast:Irvine); *itataruca* (Mozambique Id.: Peters); *kassa* (Swahili:Ingrams); *klo* (Ewe at Keta:Irvine); *nruvi* (Mozambique Id.:Peters); *taza* (Bajun of Lamu:*fide* "Ngamba," 1932: The Field:159:421).

Illustrations. The finest colored plates of this turtle, dorsal and ventral views, are those in Sowerby and Lear (1872:pls. lix-lx).

Description.[1] Snout short; beak not hooked, without cusps; edge of jaws apparently smooth; prefrontals elongate, a single pair; frontal azygous, small; frontoparietal large; parietals 2; supraocular rather large; postoculars 4; supratemporals 2; forelimb with moderately enlarged scales along anterior edge, behind them several rows of scales, posterior edge with a series of en-

[1] Based exclusively on a single specimen from Lamu Island (M.C.Z. 40019) and one from Madagascar (M.C.Z. 16866).

larged scales; each fore- and hindlimb with 1 claw;[1] tail short.

Carapace ovate, subtectiform (juv.) or smooth (adult), nuchal region truncate, margin serrate posteriorly; dorsal shields juxtaposed; nuchal broader than long, not in contact with first costals, not in contact with second marginals; vertebrals 5, first much the broadest, much broader than long, the rest as broad as, or broader than long, or II to IV longer than broad; costals 4, fourth smallest; marginals 11 pairs; supracaudal divided.

Plastron anteriorly subtruncate, no obvious lateral keels; plastral shields juxtaposed; intergular moderate; brachials 2 or 3 with some smaller scales extending anteriorly; inframarginals 4, without pores; inguinal small; interanal minute or absent.

Color. Carapace of young olive to dark brown; plastron white or yellow. Crown and sides of head dark, throat yellowish; limbs above olive to brown margined with white or yellow, below pure white or yellow with a large dark blotch, or blotches, or almost entirely dark.

Carapace of adult essentially similar to that of young, but with radiating lines or marbling; plastron yellow, immaculate. Head dark above, but on the sides the shields are more conspicuously edged with yellow.

The foregoing color description of the species is general as our African material is so scanty. For more detailed descriptions consult Deraniyagala (1939:228-230) or Carr (1952:348-349).

Size and Weight. Three juveniles, each about 5 inches (.127 meter) in length and weighing a lb. (.45 kilo), when received at the London Zoological Gardens in July-August, 1924, developed in the course of about 9 years and 4 months to 50 lbs. (22..68 kilos) each on November 8, 1933 (Flower:1937a).

Büttikofer (1890:1:260) mentions a Robertsport specimen as being 1 meter long by 75 cm. broad. The largest individuals from Europa Island were from 3¼ to 4 feet in length with weights up to 999 lbs. (450 kilos), *fide* Siebenrock (1906b). This is considerably in excess of the average adult weight of 336 lbs. mentioned by Gadow (1901:381).

Sexual dimorphism. Males have much the longer tails according to Voeltzkow (*in* Boettger:1913).

[1] Two claws are present on both fore- and hindlimbs of very young specimens, at which stage they correspond to *Euchelys macropus* Girard, as noted by Peters (1882a) and also observed by Deraniyagala (1939 : 224).

Breeding. On the West African coast the laying season is from September to January (Gadow:1901:382). More specifically on Rolas and San Thomé Islands it is from December to January (Greef:1885). Where the warm waters of the Gulf of Guinea break on the beaches of the northern Loango Coast, Green Turtles emerge to lay, at the beginning of the November rains. They are scarcer on the southern shores of Loango which are washed by the colder Atlantic currents.

That breeding takes place off the South African coast is adduced by Hewitt (1937e) from the occurrence of an occasional hatchling with a carapace length of 50 mm. and umbilical scar still unhealed.

In Aldabra Island lagoon the ♂ ♂ fight desperately with each other during the breeding season, the natives told Voeltzkow (*in* Boettger:1913), but at Europa Island they usually remain outside the reef, rarely visit the bay, and never come ashore. At low tide during the period — December 4th to 20th — of Voeltzkow's visit, one might observe the ♀ ♀ as black patches against the white sand of the lagoon. As night fell they began coming ashore in considerable numbers. From his vantage point on the ship Voeltzkow observed seven emerge at the same time. He notes that the turtles made numerous trial excavations without laying, and describes at some length the technique they employed. He frequently found eggs, sometimes an entire laying, decomposed, apparently as a result of heavy rain and too much moisture. This led him to conclude that Europa Id. was by no means an ideal breeding site for these reptiles. The mortality among laying ♀ ♀ was high for their corpses were encountered along the beach and among the dunes, as many as five being met with in the course of one walk. On Aldabra, said the natives, the ♀ ♀ disappear after reaching a certain age and are covered with barnacles when they return to the island for laying. This is chiefly between May and December when, at intervals of six weeks, a Green Turtle will come ashore three times, on each occasion laying as many as 125 eggs. Voeltzkow's full account should be compared with that of Cozzolino, synopsized below, as they differ in details. Probably the most detailed account of a Green Turtle laying in Africa is that of Cozzolino (1938)

whose observations were made on a small island 10° S off the Somali coast. Gravid ♀♀ appeared offshore cruising to and fro with their heads above the surface as if selecting a suitable spot to land. Landing takes place chiefly during the waxing, rarely during the waning, of the moon. On emerging from the water, leaving a characteristic imprint on the sand, each turtle makes for the more elevated portions of the beach beyond the reach of the highest tides.

As soon as the turtle reaches a suitable spot she promptly starts excavating, the sickle-shaped forelimbs alternating with the hind limbs. The former fling the sand aside, the latter throw it backwards. In a very short time the extent of the oval-shaped excavation begins to be apparent, and within twenty minutes is carried to a depth of about two feet ("60 cm."), the turtle disappearing from sight. She betrays her presence, however, by emitting a loud puffing sound that is audible to anyone with normal hearing for a distance of sixty yards (50 meters).

At this juncture a second operation commences. The sand being relatively loose at this depth, the tail tip is used to move it over a small area corresponding to the cloacal orifice.[1] Then the hind flipper, being turned inwards to form a scoop, is employed to lift out the displaced sand until a second cavity is excavated to a depth of about fifteen inches (35-40 cm.) with a diameter of from ten to twelve inches (25-30 cm.).

On completion of this second operation the turtle brings her hind limbs together to form an arc-shaped covering extending from the posterior margin of the carapace to the rim of the hole. Into the hole one or two eggs at a time are then dropped at irregular intervals of a second or two's duration. With the aid of a flashlight, which in no way disturbed the turtle, Cozzolino was able to watch the process and counted a total of 163 eggs. As soon as the full complement was laid the turtle quickly filled in the smaller, then the larger, hole with sand and briskly returned to the sea.

[1] It seems to us the turtle's action may have been misinterpreted and that the cloacal orifice was being moved about as urine was being discharged in order to bind the sand in preparation for its removal.

Cozzolino thinks that as many as 600 eggs may be laid by a single turtle during one month, basing his belief on the fact that more than 1000 eggs were present in the ovaries of the specimens he dissected. He also thinks that a ♀, though remaining in the vicinity where she first laid, never deposited subsequent batches of eggs in the immediate vicinity of the first site. He measured some of the spheroid eggs whose diameters ranged from 42-46 mm.,[1] their weights from 45-65 grams. For the first 48 hours after deposition the chalky white shells remained soft so that an egg might be dropped from a height of three feet or so without breaking. Under normal temperature conditions dehydration sets in after 48 hours, the shell shrivels and becomes brittle and the shape of the egg changes.

Incubation takes from 30 to 34 days, at which time the hatchlings struggle to the surface, sometimes taking an oblique course from the nest. This Cozzolino discovered after surrounding a nest-site with fishing net at a distance of 20 inches (50 cm.) and the turtlets appeared outside the net, usually on the seaward side. Thereafter he set his nets at a distance of 27½ inches (70 cm.) and captured about 153 hatchlings from each of three nests.

Hatching takes place at night and the young turtlets instinctively orient themselves and make for the sea. Many never reach it, however, for in crossing the beaches they are attacked by famished crustaceans. Survivors of the massacre which do reach the ocean are then preyed upon by other predators.

Longevity. Fifteen years for a Pacific Green Turtle in New York Aquarium, but only six years for an Atlantic specimen (Flower:1925b).

Enemies. On Aldabra Island hatchling turtles are preyed upon by Gray Herons (*Ardea cinerea cinerea*) and Frigate Birds (*Fregata minor aldabrensis*); sharks swallow young turtles entire and attack larger ones by biting off their flippers. Natives harpooned the adults when asleep or sunning in lagoons or along the shallower stretches of the coastline. About 3000 were annually taken at the time of Voeltzkow's visit — 1903-1905 (cf. Boettger:1913).

As only about 500 of these could be sent to Mahé, owing to the scarcity of shipping, the remainder were processed locally. The flesh, cut into strips and salted, was sun-dried for export to

[1] 35 mm. for a Liberian egg measured by Büttikofer (1890).

the Seychelles where workers favored it as an article of diet. The fat was cooked for shipment to France where it enjoyed a reputation as a remedy for chest diseases.

On Juan de Nova Island the natives have a curious way of dealing with the discarded portions of the turtles they kill. On the sloping dunes one sees a great many scaffoldings a yard or more in height, strengthened by cross sticks and the whole securely bound together by fiber. Behind the scaffolding a small bank is constructed. In front of the scaffolding an area of from one to two meters square is marked off and covered with the twigs of *Pemphis ocidula*. Upon these twigs are laid the turtle plastra; the carapaces, each overlapping the one in front, are arranged in long rows to the right and left while from the scaffolding hang the heads of the turtles. No such scaffolding was seen on Madagascar where the Sakalava Fody merely impale the discarded heads on stakes.

On Ascension Id., according to D. Krümmel (Werner:1912b), Green Turtles are captured and held in lagoons connected with the ocean. By May, when the season ends, there may be several hundred. The meat appears twice weekly in the Commandant's mess, and one or more turtles are presented to each visiting warship.

The use of sucker fish (*Remora remora*) to capture turtles has long been practiced on the coast of East Africa from Mombasa to Natal. The earliest references appear to be those of Andrew Sparrman who, on his return from Natal, briefly described (1787)[1] how the natives, having attached one cord to the fish's head and another around the tail, released the *remora* in the sea in the vicinity of a turtle. As soon as the fish attached itself to a turtle, both fish and reptile were drawn to the boat where the reptile could be seized or harpooned. Sparrman wrote that turtles were hunted in similar fashion on the coasts of Madagascar.

During a voyage from the Cape to Ethiopia, Henry Salt stopped at Mesuril (as Masuril), a village in Mozambique harbour. There, on September 9, 1809, he was presented with a large example of *Echeneis naucrates* which the Bishop of Mesuril

[1] For all *Remora* references see the extensive bibliography by E. W. Gudger, 1919, American Nat., **53**, pp. 520-525.

informed him would attach itself to the plastron of a turtle with such tenacity that the reptile rarely got away.

In 1829 Philibert Commerson's more detailed description of the method employed at Mozambique was published by Lacépède. Commerson states that a ring, small enough not to slip over the caudal fin, is placed about the tail of a *remora;* to the ring is attached a long cord. After this preparation the fish is placed in a receptacle, containing salt water, in the bottom of the fisherman's boat. Sail is set and the craft headed towards an area where turtles are likely to be basking on the surface. Aroused by the approaching boat, however, the lightly sleeping reptiles seek safety in diving.

It is at this juncture that the *remora* is released, and sufficient cord paid out to enable the fish to reach the turtle. Commerson states that it is only after the fish has made futile attempts to escape that it seeks shelter beneath the turtle to whose plastron it adheres by means of a sucker on its head and nape, thus enabling its employers to pull the turtle to the boat.

When returning from Pemba Island to Zanzibar, Frederic Holmwood[1] (1884) observed several fish dart out from beneath the steam launch, on which he was travelling, whenever garbage was thrown overboard. These *chazo,* as the boatmen called the fish, after feeding, returned and attached themselves to the bottom and sides of the launch. All Holmwood's efforts to pull one off by force failed, but a Zanzibari readily detached it by drawing the fish sideways. Later, Holmwood discovered that the local fishermen were accustomed to employ these *remora,* ranging in length from 2 to 4½ feet and in weight from 2 to 8 lbs., in catching turtles. He was informed that sharks and even large crocodiles were captured by this means in Malagasy waters. Between trips, the *remora* are kept in canoe-like dug-out logs stored in the huts of the fishermen who periodically change the water.

The rings worn by the fish were attached in various ways, though generally welded to a simple iron band. In some instances the band had been worn for so many years that it had become imbedded in a thick fleshy formation. One *chazo* had an extensive wound where the ring had been torn off. This fish,

[1] Holmwood, 1884, "On the Employment of the *Remora* by Native Fishermen on the East Coast of Africa." Proc. Zool. Soc. London, pp. 411-413, figs. 1-2.

said its owner, had caught the two turtles which were lying in his canoe and then affixed itself to a shark. It continued to hold on until all the spare line had been paid out and the ring torn off. The injured fish had then left the shark and returned to the boat, a by no means unusual occurrence so Holmwood was told.

Photographs of turtle hunting by means of *remora* are shown in the film "West of Zanzibar" (1954). However, the technique is not confined to East Africa, being practiced by fishermen in Chinese and Australian waters as well as in the West Indies.

In the belief that citrus leaves mitigate the pungent odor of boiling turtle flesh, it is customary in the Gold Coast to place leaves and meat together in the cooking pot. The eggs too are considered a great delicacy by the Gold Coast people. After first boiling them in sea-water the shells are perforated to drain off their watery contents, leaving the yolks. These are then baked and eaten, the taste being compared to rich cake (Irvine:1947).

Man is unquestionably the worst enemy of the Green Turtle, famous for soup though its carapace is of no commercial value. With natives everywhere hunting these turtles for their flesh and fat, besides searching for their eggs which are also highly esteemed as food, the extermination of this reptile would appear to be only a matter of time. Further information regarding their exploitation in other parts of the world will be found in Gadow (1901:382), Deraniyagala (1939:320) and Carr (1952: 353-357).

Temperament. The placidity with which a Green Turtle ignores inspection, making no attempt to bite even when touched, is commented on by Voeltzkow (*in* Boettger:1913).

Habits. Two captive Mozambique Green Turtles emitted croaking ("qakenden") sounds, says Peters (1882a).

Habitat. Green Turtles frequent the submarine "prairies à Posidonies ou Cymodocées" off the coast of Senegal, and where these occur near the shore, as at Joal, the proportion of *mydas* taken is considerable. In such areas they are captured at all seasons, though no systematic hunting takes place, being either harpooned or taken when they venture ashore during the egg-laying season (Cadenat:1949:22).

Localities. Egypt: Port Said. *Somalia:* Mogadiscio (Mogadish). *Socotra Island:* Abd el Kuri Id.; Shadwan Id. *Kenya Colony:* *Lamu Id; *Mombasa Id. (B.M.). *Tanganyika Territory:* *Dar es Salaam; Tanga. *Zanzibar Island. Mozambique:* Europa Id.; Juan de Nova Id.; Mozambique Id.; Querimba Id. *Cape Province:* Bird Id.; Cape of Good Hope; East London; Kei River mouth; Kleinemonde. *Ascension Island. Angola:* off Loanda. *Cabinda:* Chinehoxo. *Belgian Congo:* Banana at mouth of Congo River. *French Equatorial Africa:* Loango Coast. *São Thomé Island. Principe Island. Rolas Island. Gold Coast. Liberia:* Monrovia; Robertsport. *Portuguese Guinea. Senegal:* Bane d'Arguin (Argain); Hann; Joal; Mbour; other localities of questionable authenticity are listed by Rochebrune (1884a). *Cape Verde Islands:* São Vicente (Saint Vincent) Id. *Canary Islands:* Teneriffa Id.

Range. All African coasts, Indian and Atlantic oceans and — as an accidental visitor — the temperate seas.

Genus ERETMOCHELYS Fitzinger

1828. *Caretta* Ritgen (not of Rafinesque: 1814), Nova Acta Acad. Leop.-Carol., **14**, p. 270. Type: *Testudo imbricata* Linnaeus (by monotypy).

1843. *Eretmochelys* Fitzinger, Syst. Rept., p. 30. Type: *T. imbricata* Linnaeus (by original designation).

1868. *Herpysmostes* Gistel, Die Lurche Europa, p. 145. Type: *T. imbricata* Linnaeus (*fide* Mertens, 1936, Senckenbergiana, **18**, p. 75).

1873j. *Onychochelys* Gray, Proc. Zool. Soc. London, p. 397, figs. 1-2. Type: *O. kraussi* Gray = *T. imbricata* Linnaeus (by monotypy).

Definition. Head with 2 pairs of prefrontal shields; postoculars 3; claws 2.

Skull with triturating surface of maxilla ridged, the ridge strongest anteriorly, extending somewhat on to the premaxillae; premaxillae in contact with vomer which separates the maxillae; maxillae without vertical ribbing on inner surface of its cutting edge; descending processes of prefrontals in contact with vomer only; a blunt and rather low ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view not concealed by the moderate secondary palate; pterygoids deeply concave posteriorly; frontal entering orbit; crista prae-

temporalis strong; mandibular symphysis pointed, concave, as long as broad; labial margin sharp, straight, not rising to a point at the symphysis; lingual margin lower than the labial, without ridge; no symphysial ridge.

Carapace without lateral fontanelles in fully adult individuals; neurals 9-11, usually hexagonal, short-sided in front; peripherals 11 pairs, the ninth pair not in contact with the ribs; nuchal shield not in contact with first costals; costals typically 4 pairs.

Plastron with a large intergular shield; inframarginals 4 pairs, without pores.

Range. Tropical, subtropical and — as an occasional visitor — temperate oceans.

Eretmochelys imbricata (Linnaeus)

1766. *Testudo imbricata* Linnaeus, Syst. Nat., ed. 12, **1**, p. 350: American and Asiatic Seas.
1834. *Chelonia pseudo-mydas* Lesson, *in* Bélanger, Voy. Indies-Orient., Zool., p. 299: Atlantic Ocean.
1834. *Chelonia pseudo-caretta* Lesson, *in* Bélanger, Voy. Indies-Orient., Zool., p. 302: Atlantic Ocean.
1835. *Caretta Bissa* Rüppell, Neue Wirbelth. Fauna Abyss., Amphib., p. 4, pl. ii: Red Sea.
1922a. Mertens, 168 (lists type, as syn. of *imbricata*).
1835. *Chelonia imbricata* Temminck and Schlegel, p. 13, pl. v.
1872. Sowerby and Lear, pls. lvii-lviii.
1875. Melliss, 99.
1882a. Peters, 17.
1890. Büttikofer, **2**, 438, 478.
1896a. Bocage, 98.
1906a. Mocquard, 481.
1909a. Siebenrock, 547.
1913c. Nieden, 55.
1921d. Loveridge, 51.
1849. *Caretta imbricata* A. Smith, App., 2.
1873b. Gray, 92.
1884a. Rochebrune, 39.
1857. *Eretmochelys squamata* Agassiz, Contr. Nat. Hist. U. S., **1**, p. 382: Indian and Pacific Oceans.
1858. *Caretta squamosa* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 442, pl. xxx, figs. 1-7: Sulu Seas and Indian Ocean.

1858. *Caretta rostrata* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 446, pl. xxx, figs. 8-13: Fiji Islands.
1873j. *Onychochelys kraussi* Gray, Proc. Zool. Soc. London, p. 398, figs. 1-2: Atlantic Ocean off French Guiana.
1885. *Chelone imbricata* Greef (1884), 49, footnote.
1889a. Boulenger, 183.
1893a. Boettger, 12.
1896. Tornier, 3.
1897. Tornier, 63.
1898. Sclater, W. L., 97.
1898. Tornier, 283.
1900b. Tornier, 582.
1901. Gadow, 385.
1901. Steindachner, 326.
1903a. Boulenger, 92, 96.
1906i. Boulenger, 197.
1906. Johnston, 819, 833.
1910. Sternfeld, 5, fig. 10.
1911d. Sternfeld, 51.
1914. Fuchs, 1914, pp. 1-325, figs. 1-182, pls. i-vi.
1923g. Loveridge, 933.
1924b. Loveridge, 3 (as *impricata*)
1925b. Flower, 932.
1929. Rose, 184.
1930a. Scortecci, 215.
1931. Ingrams, 429.
1937b. Angel, 1696.
1955. Cansdale, 96, 104.
1929. *Eretmochelys imbricata* Flower, 39.
1929. Lindholm, 287.
1933. Flower, 750.
1933h. Loveridge, 207.
1937a. Flower, 13.
1937e. Hewitt, 16, pl. ivB.
1937f. Loveridge, 488.
1947. Irvine, 311.
1949. Cadenat, 16.
1949. Villiers, 165.
1950. Rose, 327.
1950. Williams, 552.
1952. Williams and McDowell, pl. i, fig. 4.
1934a. *Eretmochelys imbricata imbricata* Mertens and Müller *in* Rust, 10.
1934a. *Eretmochelys imbricata squamosa* Mertens and Müller *in* Rust, 10.

Common names. Hawksbill Turtle (English); *anyite* (Ewe: Irvine); *apuhuru* (Fante:Irvine); *ayikplonto* (Ga:Irvine); *baga* for ♀, *bissa* for ♂ (Arabic in Red Sea:Rüppell); *hala-apatadzi* (Ga:Irvine, *q. v.* for other Gold Coast names); *ingappa* (Mozambique:Peters); *ngamba* (Cape Delgado Island:Peters; Zanzibar:Ingrams).

Illustrations. A reasonably good colored plate will be found in Rüppell (1835), and very fine ones of a subadult in Sowerby and Lear (1872b:pls. lvii-lviii).

Description. (Based exclusively on six African and Malagasy specimens in the Museum of Comparative Zoology).

Snout elongate, compressed; beak drawn out but not hooked, without cusps; edge of jaws apparently smooth; prefrontals not elongate, in 2 pairs; frontal azygous, small, rarely[1] fused with frontoparietal; frontoparietal large, entire or semidivided anteriorly; parietals 2, transverse in juveniles, somewhat elongate in adults; a small interparietal sometimes present; supraocular rather large; postoculars 3, rarely[2] 4; supratemporals 2 or 3, one sometimes fused with a temporal; forelimb with moderately enlarged scales along anterior edge, behind them several rows of scales, posterior edge with a series of enlarged scales; both fore- and hind limbs with 2 claws; tail short.

Carapace ovate, subtectiform in adults, with 3 interrupted keels in young but only a trace of the lateral ones persisting in adults, nuchal region truncate, margin weakly serrate in young, strongly in adults; dorsal shields juxtaposed in hatchling, imbricate in adults, juxtaposed in aged individuals; nuchal broader than long, not in contact with first costals, not in contact with second marginals; vertebrals 5, exposed portion of each broader than long at all ages, the first no broader than the others in young, broader than the others in adults; costals 4, fourth smallest; marginals 11 pairs; supracaudal divided.

Plastron anteriorly rounded, 2 prominent lateral keels; plastral shields of adult more or less imbricate; intergular moderate; brachials 2 or 3 with some smaller scales extending anteriorly; inframarginals 4, without pores; inguinal small; interanal minute or absent.

[1] Fused in a Zanzibar specimen (M.C.Z. 1141) and a Malagasy turtle (M.C.Z. 16867).

[2] Four in a Zanzibar specimen (M.C.Z. 1141).

Color. Carapace of young light brown flecked with darker, or black blotched with lighter; plastron substantially similar. Head and limbs light brown to black, more or less uniform.

Carapace of adult horn to reddish brown heavily marbled or streaked with black; plastron yellow, the posterior portion of each shield blotched with black. Head and limbs dark above, but on the sides and below yellow heavily blotched with black.

The foregoing color description is based solely on our African and Malagasy material.

Size. Carapace length of largest in the Paris Museum 740 mm.; surpassed by one of Rüppell's "*bissa*" which was 765 mm., by 690 mm. broad; the lectotype was only 750 mm., by 635 mm. broad; the record is apparently 850 mm. (B.M.).

Breeding. On Rolas and São Thomé Island the ♀ ♀ come ashore to lay from December to February (Greef:1885). In the Red Sea region they lay from February to March; after laying, the ♀ ♀ regularly return to the site, according to Rüppell (1835).

Longevity. Fifteen years, 7 months, 28 days, and still alive about 1937 (Flower:1937a). The alleged record of 32 years, quoted by Gadow (1901:386), has been traced to Tennant (1861:294), who quoted Bennett (1843:275) who followed it back to 1826 and 1794 (Flower:1925b, where full references to preceeding citations will be found).

Enemies. In Liberia it is eaten by the Africans but not by Europeans (Johnston:1906). The plates of the ♂ ♂ are thinner than those of the ♀ ♀, and consequently are of less value commercially (Rüppell:1835). Between 700 and 800 kilograms of high grade tortoise-shell was annually taken from the Hawksbill Turtles in the vicinity of Cape Delgrado (Peters:1882a). As much as 8 lbs. of shell may be removed from a single large specimen (Gadow:1901). Great numbers of stripped carapaces were observed around the natives' huts on Abd el Kuri Island by H. O. Forbes, who remarks that though it still occurs off the coast of Socotra Island it is not nearly so common as it was eighteen centuries ago when it was an article of trade much sought after by merchants from Arabia (Boulenger:1903a).

Temperament. In marked contrast to the Green Turtle, the Hawksbill bites so freely that Malagasy fishermen carry in their

boats a piece of wood which they hold out to a harpooned turtle. Once the reptile has seized the proffered wood it does not readily let go. If this procedure is not followed, so the men told Voeltzkow (*in* Boettger:1913), the turtle is apt to bite on their frail craft when being hauled aboard, and may inflict considerable damage.

Localities. Egypt: Saint John Id.; Red Sea coasts from Zebejir to Zukur. *Eritrea:* Massaua. *Socotra Island:* Abd el Kuri Id.; Socotra Id. *Kenya Colony:* Frere Town; *Mombasa Id. *Tanganyika Territory:* Dar es Salaam; Lindi; Tanga. *Zanzibar Island:* *Zanzibar. *Mozambique:* Cape Delgado; Mozambique Id.; Querimba Id. near Ibo. *Cape Province:* False Bay; Simonstown Beach; Table Bay. *Ascension Island:* *(M.C.Z. 4095). *French Equatorial Africa:* Gabon Coast (P.M.). *São Thomé Island. Principe Island:* Rolas Id. (only). *French Cameroon:* Longuy (Longji). *Gold Coast:* *Tenia (B.M.). *Liberia:* Angel River. *Sierra Leone:* *Bonthé, Bonthé district. *Senegal:* Banc d'Arguin (Argain); Joal (Joalles); other localities of questionable authenticity are listed by Rochebrune (1884a). *Cape Verde Islands:* Fogo Id.

Range. East, South and West coasts of Africa, Indian and Atlantic oceans and — as an accidental visitor — the temperate seas.

Genus CARETTA Rafinesque

1814. *Caretta* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66. Type: *C. nasuta* Rafinesque = *Testudo caretta* Linnaeus (by monotypy).

1835. *Thalassochelys* Fitzinger, Ann. Wiener Mus., **1**, pp. 110, 121, 128. Type: *T. caouana* Fitzinger = *T. caretta* Linnaeus (designation by Fitzinger, 1843).

1838. *Caouana* Cocteau, Rept. in De la Sagra, Hist. Fis. Pol. Nat. Cuba, **4**, p. 31. Type: *T. cephalo* Schneider = *T. caretta* Linnaeus (by monotypy).

1843. *Halichelys* Fitzinger, Syst. Rept., p. 30. Type: *H. atra* Fitzinger = *T. caretta* Linnaeus (by original designation).

1873j. *Cephalochelys* Gray, Proc. Zool. Soc. London, p. 408. Type: *C. oceanica* Gray = *T. caretta* Linnaeus (by monotypy).

1873j. *Eremonia Gray*, Proc. Zool. Soc. London, p. 408. Type: *E. elongata* Gray = *T. caretta* Linnaeus (by monotypy).

Definition. Head with 2 pairs of prefrontal shields; postoculars 3; claws 2.

Skull with triturating surface of maxilla *not* ridged; premaxillae not reached by vomer which does not separate the maxillae; maxilla without vertical ribbing or a sharp cutting edge, its whole surface sloping dorsomedially as part of a large crushing surface; descending processes of prefrontals in contact with vomer and palatines; a blunt ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view concealed by the extensive secondary palate; pterygoids deeply concave posteriorly; frontal excluded from orbit; crista praetemporalis strong; mandibular symphysis rounded, concave, longer than broad; neither labial nor margins raised as cutting edges; no symphysial ridge.

Carapace without lateral fontanelles in adults; neurals 7-11, occasionally some separated, typically hexagonal, short-sided in front; peripherals 12-13 pairs, the ninth or tenth pair not in contact with the ribs; nuchal usually in contact with first costals; costals typically 5 pairs.

Plastron without, or with only a very small, intergular shield; inframarginals 3 pairs, without pores.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

Caretta caretta (Linnaeus)

1758. *Testudo Caretta* Linnaeus, Syst. Nat., ed. 10, 1, p. 197: Islands off America.

1783. *Testudo Cephalo* Schneider, Naturg. Schildkröten, p. 303: No locality.

1788. *La Caouane* Lacépède, Hist. Nat. Quad. ovip. Serpens, 1, p. 95; and *Testudo caouana* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Jamaica, British West Indies (restricted).

1788. *La Tortue nasicorne* Lacépède, Hist. Nat. Quad. ovip. Serpens, 1, p. 103; and *Testudo nasicornis* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: America.

1814. *Caretta nasuta* Rafinesque, Specchio Sci. (Palermo), 2, No. 9, p. 66: Sicily (*fide* Lindholm: 1929).

1820. *Caretta atra* Merrem, Vers. Syst. Amphib., p. 17: Ascension Island.

1833. *Chelonia pelasgorum* Valenciennes, pl. vi, *in* Bory de Saint Vincent, Expéd. sci. de Morée, Zool.: Modon, etc., Mediterranean Sea.

1844. *Caouana elongata* Gray, Cat. Tortoises Brit. Mus., p. 53: No locality.
1858. *Thalassochelys corticata* Girard, U. S. Explor. Exped. 1838 1842, Herp., p. 431, pl. xxix: Madeira Islands.
1894. Oliver, 100.
1896b. Oliver, 118.
1862a. *Chelonia corticata* Strauch, 19.
1903. Mayet, 9.
1873j. *Cephalochelys occanica* Gray, Proc. Zool. Soc. London, p. 408: ? Mexico.
1884a. *Caouana caretta* Rochebrune, 38.
1887. *Thalassiochelys tarapacona* (*sic*) Philippi, Zool. Garten, **28**, p. 85: Iquique, Chile (identified by subsequent description. See Philippi, 1899).
1889a. *Thalassochelys caretta* Boulenger (part), 184.
1891c. Steindachner, 305, 306.
1893a. Boettger (part), 13.
1895a. Bocage, 6.
1896a. Bocage, 66.
1898. Jeude, 11.
1898. Selater, W. L., 97.
1901. Gadow (part), 326, 387, figs. 69, 84 (diagrams based on a misconception involving young of one species, adults of another).
1902. Bocage, 208.
1903a. Boulenger, 96.
1906a. Mocquard, 481.
1912a. Pellegrin, 256.
1923g. Loveridge, 933.
1924b. Loveridge, 3.
1925. Flower, 932.
1926c. Pellegrin, 49.
1929. Rose, 184, fig. 122.
1932d. Witte, 57.
1899. *Thalassochelys tarapacana* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 731 (validating redescription).
1899. *Chelonia Caouana* Doumergue, 253.
1909a. *Caretta caretta* Siebenrock, 549.
1911d. Sternfeld, 52, fig. 64.
1912b. Werner, 465.
1929. Flower, 39.
1929. Lindholm, 287.
1933. Flower, 751.
1934. Mosauer, 52.

1937b. Angel, 1696.
1937a. Flower, 14, 37.
1937e. Hewitt, 15, pl. ivB.
1949. Cadenat, 17, figs. 4, 5, 7-12, 15b, 16a.
1949. Villiers, 165.
1950. Rose, 327, fig. 127.
1950. Williams, 552.
1930. *Caretta* [*caretta* inferred] Babcock (part), 95.
1933. *Caretta gigas* Deraniyagala, Ceylon Jour. Sci., Sect. B, **18**, p. 66, figs. 4-6, pl. v: Gulf of Mannar, Ceylon.
1934a. *Caretta caretta caretta* Mertens and Müller *in* Rust, 10.
1935. *Tortue caret* Witte, 94.
1939. *Caretta caretta gigas* Deraniyagala, 162.

Common names. Red-brown Loggerhead (English); *fahroun el barr* (in Tunisia:Mosauer); *nduvi* (at Lindi:Loveridge MS).

Description.[1] Snout relatively short, not compressed; beak distinctly hooked, unicuspid; edge of jaws apparently smooth; prefrontals not elongate, in 2 pairs with an additional central pair; frontal azygous, small, longer than broad; frontoparietal large, as broad as long, semidivided posteriorly; parietals not elongate, broken up; supraocular moderately large; postoculars 3; supratemporals in 3 pairs; forelimb with moderately enlarged scales along anterior edge, behind them numerous small scales, posterior edge with a series of distinctly enlarged scales; both fore- and hind limbs with 2 claws; tail moderately short.

Carapace ovate, tectiform, with a strong interrupted vertebral keel and nearly obsolescent lateral keels (in the young Madeira specimen); nuchal region truncate, margin somewhat serrate; dorsal shields juxtaposed; nuchal broader than long, in contact with first costals on right side, excluded on left; vertebrals 6, first smallest;[2] costals 5, first smallest; marginals 13 pairs; supracaudal divided.

Plastron anteriorly rounded, 4 strong, obtuse, interrupted, lateral keels; plastral shields juxtaposed; intergular present, small; brachials 3 with some smaller scales extending anteriorly; inframarginals 3, without pores; inguinal absent; interanal absent.

Color. Carapace reddish brown,[3] points of keels and marginals

[1] Based on the almost foot-long, Madeiran type of *T. corticata* Girard (U.S.N.M. 7778) examined by E. E. W.

[2] The normal first vertebral in the type of *corticata* (U.S.N.M. 7778) is asymmetrically divided.

[3] In the now dried type of *corticata* more uniformly reddish than described by Girard.

lighter; plastron whitish yellow to yellowish brown. Head scales reddish centrally, narrowly margined with yellow; eyelids conspicuously black (*fide* Doumergue); neck yellowish; throat yellowish brown; limbs above, reddish brown, below, yellowish brown.

Size and Weight. In the almost complete absence of African material we offer the following remarks.

The carapace of a Florida loggerhead at hatching had a length of about 48 mm., a breadth of 35 mm., and a weight of about 20 grams. When four-and-a-half years old this turtle weighed 81½ lbs. (37 kilos.) and its carapace measured about 2 feet (630 mm.) in length, and 1 foot, 11 inches (590 mm.) in breadth. Its rate of growth was much more rapid than that of three other loggerheads reared under almost similar conditions. Yet all three revealed that these turtles attain to maturity much more rapidly than was generally supposed (Parker:1939).

Carapace length of a hatchling (M.C.Z. 4017) from Key West, Florida, 49 mm., breadth 41 mm., length of forelimb from axilla to tip, 35 mm.; the carapace length being contained in that of the forelimb .71 per cent.

Carapace length of a young turtle (M.C.Z. 28202) from Bermuda, 83 mm., breadth 72 mm., length of forelimb from axilla to tip 65 mm.; the carapace length being contained in that of the forelimb .79 per cent.

Carapaces rarely exceed 700 mm. in length at Oran (*fide* Doumergue:1899). Carapace lengths of adults from Hann and Joal, Senegal, were 1040 and 1080 mm., respectively (Cadenat: 1949:19).

Carapace length *over the curve* of the largest known "*gigas*" ♂, from China (*fide* Fang:1934 *in* Deraniyagala: 1939), 940 mm.; largest "*gigas*" ♀ from Moratuva, Ceylon 960 mm. (*fide* Deraniyagala:1939:183).

Longevity. Possibly 33 years in the Vasco da Gama Aquarium in Lisbon, where several lived from 1898 until 1931, when they succumbed during a spell of exceptionally hot weather (*fide* Dr. Rodrigo Boto, who so informed Flower:1937a). Another loggerhead, whose age when received at the Berlin Zoological Gardens in September, 1913, was estimated at 2 years, was still alive on September 19, 1936. Consequently the animal was at least 23, possibly 25, years old.

Diet. In spring, loggerheads appear within the narrow sandbar on the west coast of Lanzarote Island in order to feed on the abundant mussels (*Gari depressa,* recorded as *Psammobia vespertina,* and *Venus verrucosa*) which occur there (Steindachner: 1891c).

Enemies. The flesh of the caouanne is good to eat, according to Doumergue (1899).

Localities. French Morocco: Mogador. *Algeria:* Oran. *Tunisia:* Bizerte; Gabes; Sfax market; Tunis. *Egypt:* Alexandria; Brullos; Damietta; Port Said. *Socotra Island:* Abd el Kuri Id.; Bandar Saleh. *Kenya Colony* (Loveridge:1923g). *Mozambique:* *Inhambane (U.S.N.M.). *Cape Province:* Kalk Bay; Muizenberg; Peddie Coast. *Southwest Africa. Ascension Island. Belgian Congo:* Banana. *French Equatorial Africa:* Gabon. *Ivory Coast:* San Pedro. *Senegal:* Fadiouth; Hann; Joal. *Rio de Oro* (*fide* Carr:1952:383, but Cameroons may be included on basis of *Lepidochelys,* which see). *Cape Verde Islands:* Sal Id. near São Vicente Id. *Canary Islands:* Lanzarote Id.; Teneriffa Id. *Madeira Islands:* Madeira Id.

Range. All African coasts, Indian and Atlantic oceans, the Mediterranean and — as an accidental visitor — the temperate seas.

Genus LEPIDOCHELYS Fitzinger

1843. *Lepidochelys* Fitzinger, Syst. Rept., p. 30. Type: *Chelonia olivacea* Eschscholtz (by original designation).

1880. *Colpochelys* Garman, Bull. Mus. Comp. Zool., **6**, p. 124. Type: *kempi* Garman (by monotypy).

Definition. Head with 2 pairs of prefrontal shields; postoculars 3-4; claws 2-3 (though adults sometimes have only 1).

Skull with triturating surface of maxilla ridged, the ridge subequal in height throughout, not extending on to the premaxillae; premaxillae in contact with vomer which separates the maxillae; maxilla without vertical ribbing on inner surface of its cutting edge; descending processes of prefrontals in contact with vomer only; no obvious ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view not concealed by the moderate secondary palate; pterygoids deeply concave posteriorly; frontal entering orbit; crista praetemporalis

strong; mandibular symphysis pointed, about as long as broad; labial and lingual margins slightly raised into cutting edges; a more or less distinct symphysial ridge.

Carapace without lateral fontanelles in adults; neurals 12-15, some quadrate, others hexagonal, short-sided in front; peripherals usually 12-13 pairs, the tenth pair not in contact with the ribs; nuchal shield usually in contact with first costals; costals 5 or more pairs.

Plastron without, or with only a very small, intergular shield; inframarginals 4 pairs, each with a pore near its posterior edge.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

Lepidochelys olivacea olivacea (Eschscholtz)

1820. ?*Chelonia multiscutata* Kuhl, Beitr. Zool. Anat., p. 78: No locality.
1829. *Chelonia olivacea* Eschscholtz, Zool. Atlas, p. 3, pl. iii: Manila Bay, Philippine Islands, China Sea.
1860. Duméril, 170.
1835. *Chelonia Dussumierii* Duméril and Bibron, Erpét. Gén., **2**, p. 557, pl. xxiv, figs. 1-1a: China Sea and Malabar Coast.
1835. *Caretta olivacea* Rüppell, 7, pl. iii.
1839. Parker, 129.
1949. Cadenat, 17, 23, figs. 6, 16b.
1844. *Caouana Rüppellii* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 53: ? India (*nomen nudum*).
1849. *Caouana dessumierii* (*sic*) A. Smith, App., 2.
1857. *Chelonia polyaspis* Bleeker, Nat. Tijdshr. Ned. Indies, **14**, p. 239: Batavia, Java.
1884a. *Caouana olivacea* Rochebrune, 38.
1888a. *Thalassochelys olivacea* Boettger, 18.
1889a. *Chelonia dubia* Bleeker (*nomen nudum*) in Boulenger, Cat. Chelon. Rhyncho. Crocod. Brit. Mus., p. 186: Borneo.
1899. *Thalassochelys controversa* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 732: No locality.
1900b. *Thalassochelys caretta* Tornier (not of Linnaeus), 582.
1902c. Tornier, 665 (head lost, but hatchlings studied by us).
1910. Sternfeld, 5 (based on the 1902c material just mentioned).
1913c. Nieden, 55.
1930a. Scortecci, 215.
1908. *Caretta remivaga* Hay, Proc. U. S. Nat. Mus., **34**, p. 194, pl. x, figs. 1-3, pl. xi, fig. 5: Ventosa Bay, Gulf of Tehuantepec, Mexico.

1934a. *Caretta caretta olivacea* Mertens and Müller *in* Rust, 10.
1937f. Loveridge, 488.
1943. *Lepidochelys olivacea olivacea* Deraniyagala, 81, 92, figs. 1, 3a, 5a, 6a.

Common names. Olive Loggerhead (English); *bage* (in Eritrea:Rüppell).

Illustrations. A clear and detailed drawing of the dorsal view, together with a lateral view of the head and plastron from below, is furnished by Rüppell (1835).

Description.[1] Snout relatively short, not compressed; beak scarcely or slightly hooked, not or but slightly bicuspid (tricuspid in Rüppell's figure); edge of jaws apparently smooth; prefrontals not elongate, in 2 pairs;[2] frontal azygous, small, as broad as, or broader than, long (in hatchlings), longer than broad (in adult); frontoparietal large, broader than long, semi- or wholly divided; parietals transverse (in hatchlings), elongate (in adult), or somewhat broken up (in either); supraocular moderately large; postoculars 3-4; supratemporals broken up; forelimb with moderately enlarged scales along its anterior edge, behind them several rows of scales, posterior edge with a series of distinctly enlarged scales; both fore- and hind limbs with 2 claws, though on the former scarcely distinguishable; tail short.

Carapace ovate, hardly tectiform, with a weak, interrupted, vertebral keel, in hatchlings similar lateral keels are also present, nuchal region truncate, margin scarcely serrate; dorsal shields juxtaposed; nuchal broader than long, normally[3] in contact with the first costals, not in contact with second marginals; vertebrals 5-7, in hatchlings all broader than long except the last which is usually longer than broad, in adults I is somewhat broader than long, II-VI as long as, or longer than, broad, VII much the broadest; costals[4] 6 or 7,[5] first smallest; marginals 12 pairs;

[1] Based on five hatchlings from the Cameroon (Berlin Mus. 15513), three hatchlings from the Gabon (Paris Mus. 41.58) and Rüppell's (1835) figures and description of a Massaua specimen. Checked on nine hatchlings from Ceylon; India; New Britain and Mexico, but their deviations are not included in this description.

[2] The second pair of frontals are fused with the supraocular on one or both sides in three of the five Cameroon hatchlings.

[3] Nuchal separated from first costal by a marginal in one Cameroon hatchling.

[4] Of the five Cameroon hatchlings two have 5 costals on both sides; one has 5 on the right, 6 on the left; two have 6 on both sides. The series, obviously from one nest, must be regarded as intergrades between *L. o. olivacea* (Eschscholtz) and *L. o. kempi* (Garman). Incomplete supernumerary costals, split off from the larger complete ones, occur in the Gabon hatchlings; we have not included these incomplete scutes in the costal count.

[5] Seven in a Senegal specimen (Cadenat:1949).

supracaudal divided.

Plastron anteriorly rounded, 2 obtuse, interrupted, lateral keels; plastral shields juxtaposed; intergular small, rarely divided [1] or absent; brachials 2-3 with some subequal or smaller shields extending anteriorly; inframarginals 4, each with or without a small pore posteriorly; inguinals minute or absent; interanal minute or absent.

Color. Carapace of hatchlings (from Gabon) uniformly olivaceous black, or (in Cameroon intermediates) wholly black; plastron, head and limbs suffused with brown.

Carapace of adult (from Massaua, Rüppell:1835) olive green; plastron sulphur yellow. Head, neck and foot above, olive green; below sulphur yellow. Iris dark brown, eyeball blue-gray.

Size. Carapace lengths and breadths of five hatchlings from Cameroon (Berlin Mus.) range from 42 x 38 to 44 x 40 mm., those of three hatchlings from Gabon (Paris Mus.), 49 x 45, 50 x 44 and 50 x 45 mm., respectively. This will give some idea of the variation in length to breadth ratio in hatchlings that almost certainly came from only two broods. Rüppell's Massaua turtle was said to be 630 mm. in length as well as breadth. Carapace lengths of specimens from Ngaparo and Joal, Senegal, were 660 and 690 mm. respectively (Cadenat:1949), while the possible maximum length for an adult may be 790 mm.; breadth 680 mm. (*fide* Deraniyagala:1939).

Breeding. In May on the Eritrean coast (Rüppell:1835).

Localities. Egypt? Eritrea: Massaua. *Socotra Island. Tanganyika Territory:* Lindi. *Cape Province:* Table Bay. *Belgian Congo:* Banana; Moanda (Royal Museum of the Belgian Congo, *fide* Carr *in litt.*). *French Equatorial Africa:* Gabon Coast, *British Cameroon:* *Victoria (intermediates *olivacea* × *kempi*). *Gold Coast:* *Tenia (B.M.). *Ivory Coast:* (Paris Mus.). *Senegal:* Goree Id.; Guet N'Dar; Hann, Joal; Ngaparo.

Range. East, South and West coasts of Africa, Indian and Pacific Oceans, also — as an accidental visitor — the temperate seas.

From the Azores we have seen a young *L. o. kempi* (Monaco Mus. 2660), taken by the Prince of Monaco in 1913, while hatch-

[1] Divided on a Cameroon (Berlin Mus.) and on a Gold Coast hatchling (Brit. Mus.) seen by us.

lings from the Cameroons (Z.M.U. 15513) must be considered intermediates between the two races (see footnote to p. 497).

Family DERMOCHELYIDAE

1902. *Dermochelyidae* Wieland, Amer. Jour. Sci., (4), **14**, p. 107.

Definition. Cryptodirous testudinates adapted to a marine life. Horny shields present in young, replaced in adults by smooth skin.

Skull without nasal bones; prefrontals in contact dorsally, with descending processes that are moderately separated; temporal region hardly emarginate posteriorly; parietal meeting squamosal; postorbital very large; no bones tending to be reduced; quadrate not enclosing stapes; postotic antrum absent; parietals without descending processes; upper jaw without ridges on its triturating surface; vomer present, separating palatines; mandible without a coronoid bone.

Neck vertebrae with only one biconvex centrum — the fourth, typically an articular connection between the sixth and seventh centra, the eighth centrum concave in front, doubly or not; coracoids with their median borders not expanded; humerus of an exaggerated marine type with deltopectoral crest very far down the shaft; trochanteric fossa of femur reduced by union of the trochanters; phalanges without condyles; claws absent.

Carapace with epithecal component very strongly developed, represented by a mosaic of small bones; thecal carapace and plastron greatly reduced, not directly united; neither carapace nor plastron hinged; pleural bones reduced to the endochondral ribs, separated by wide fenestrae; peripherals absent; nuchal a butterfly-shaped bone with a ventral attachment surface for the eighth vertebra; neural bones absent, represented only by the neural arches of the vertebrae; pygals absent; plastron reduced to a narrow ring of bones surrounding a great fontanelle; entoplastron absent.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

Genus DERMOCHELYS Blainville

1816. *Dermochelys* Blainville,[1] Bull. Soc. Philom. Paris, p. "111" (misprint = 119). Type: *Testudo coriacea* Linnaeus (by monotypy in Cuvier: 1829).

1820. *Sphargis* Merrem, Vers. Syst. Amphib., p. 19. Type: *T. coriacea* Linnaeus (by monotypy).

1822. *Coriudo* Fleming, Phil. Zool., **2**, p. 271. Type: *T. coriacea* Linnaeus (by monotypy).

1828. *Seytina* Wagler, Isis von Oken, p. 861. (Substitute name for *Sphargis* Merrem.)

1830. *Dermatochelys* Wagler, Natur. Syst. Amphib., p. 133. (Emendation for *Dermochelys*.)

1832. *Chelyra* Rafinesque, Atlantic Jour., **1**, p. 64. Type: *T. coriacea* Linnaeus (by monotypy).

Definition. Similar to that given under DERMOCHELYIDAE, the family being monotypic.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

DERMOCHELYS CORIACEA (Linnaeus)

1766. *Testudo coriacea* Linnaeus, Syst. Nat., ed. 12, **1**, p. 350: Mediterranean Sea.

1789. Poiet, 283.

1802b. Daudin, 62, pl. xviii, fig. 1.

1771. *Testudo areuata* Catesby, Nat. Hist. Carolina, **2**, p. 40: Coasts of Carolina and Florida (by inference).

1788. *Le Luth* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, p. 111; and *Testudo lyra* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Barbary Coast.

1792. *Testudo tuberculata* Schoepff, Hist. Testud., p. 144: No locality.[2]

1814. *Chelonia lutaria* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66: Sicily (*fide* Lindholm: 1929).

1820. *Sphargis mercuralis* Merrem, Vers. Syst. Amphib., p. 19: Mediterranean Sea and Atlantic Ocean.

[1] In the same year *Dermochelys* was also proposed by Blainville in Jour. Phys. Chim. Hist. nat. (Paris), **83**, p. 259. We cannot say which publication had priority, but it is the Bulletin that is currently cited by herpetologists. In neither paper was *any* species mentioned. However, *coriacea* Linnaeus was the only included species assigned to *Dermochelis* (*sic*) by Cuvier (1829, Regné Animal, ed. 2, **2**, p. 14) and this has been accepted as the type by the "Official List of Generic Names in Zoology."

[2] Attributed by Schoepff to Pennant, 1771, Philos. Trans. Royal Soc. London, **61**, p. 271 (*not* 275), pl. x, figs. 4-5, but Pennant merely provides an English name — Tuberculated Tortoise — to a specimen which he thinks may be *Testudo coriacea* Linnaeus. In Schoepff's 1801 ed. *tuberculata* appears on p. 123.

1835. Temminck and Schlegel, 6, pls. i-iii.
1849. Smith, A., App., 2.
1829. *Dermochelis Atlantica* Lesueur, in Cuvier, Regné Animal, **2**, p. 14, footnote: No locality (*nomen nudum*).
1830. *Dermatochelys porcata* Wagler, Natür. Syst. Amphib., pl. i, figs. 1-23: No locality (uses *coriacea* in text, p. 133).
1862a. *Sphargis coriacea* Strauch, 19.
1872. Gervais, p. 199, pls. v-ix.
1873b. Gray, 96.
1884a. Rochebrune, 40.
1894. Oliver, 101.
1896. Doumergue, 477.
1896b. Oliver, 118.
1899. Doumergue, 255.
1933. Heldt, 1-40, figs. 1-17.
1949. Cadenat, 16, fig. 13.
1844. *Sphargis coriacea* var. *Schlegelii* Garman, U.S. Nat. Mus. Bull., **25**, pp. 295, 303: Tropical Pacific and Indian Oceans.
1889a. *Dermochelys coriacea* Boulenger, 10.
1890. Büttikofer, **1**, 266; **2**, 437, 478, fig.
1893c. Matschie, 208.
1899. Sclater, 96.
1901c. Tornier, 66.
1906a. Mocquard, 483.
1909a. Siebenrock, 553.
1911b. Sternfeld, 52.
1925b. Flower, 918.
1929. Lindholm, 287.
1929. Rose, 184.
1933. Flower, 752.
1937e. Hewitt, 16, pl. ivB.
1937f. Loveridge, 488.
1947. Irvine, 312.
1949. Villiers, 165, fig.
1950. Rose, 327.
1950. Williams, 552.
1955. Cansdale, 97, 104.
1899. *Sphargis angusta* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 730, pl. i: Tocopilla, Chile.
1901. *Dermatochelys coriacea* Gadow, 325, 333, fig. 73.
1906. *Dermochelis coriacea* Johnston, 819, 833.
1934a. *Dermochelys coriacea coriacea* Mertens and Müller *in* Rust, 10.
1934a. *Dermochelys coriacea schlegeli* Mertens and Müller *in* Rust 10.

Common names. Leatherback; Leathery Turtle; Luth or Trunk Turtle (English); *bosange* (Ga:Irvine, whom see for other Gold Coast names); *noa* (Swahili at Lindi:Loveridge MS).

Illustrations. Those of Temminck and Schlegel (1835:pls. i-iii) are quite good.

Description. (Based exclusively on a juvenile (M.C.Z. 21055) from the Guinea Coast, West Africa.)

Snout moderate; beak deeply notched in middle, strikingly bicuspid; edge of jaws denticulate; prefrontals in 2 pairs, of which the posterior pair may be broken up; frontal broken up; frontoparietal large; parietals, supraocular, postoculars, and supratemporals broken up; forelimb with slightly enlarged scales along anterior edge, behind them many rows of smaller scales, posterior edge without noticeably enlarged scales; both fore- and hind limbs clawless; tail short.

Carapace a mosaic of small polygonal plates, 7 longitudinal rows of which are enlarged to form conspicuous ridges, ovate, slightly arched, posteriorly prolonged into a caudal point.

Plastron also a mosaic of polygonal plates, 5 longitudinal rows, of which the median is double, forming conspicuous keels, anteriorly truncate, posteriorly pointed.

Color. Of juvenile from Guinea coast. Carapace and plastron black, each keel tipped with yellow; crown and sides of head dark, throat yellowish; limbs black narrowly edged with yellow.

Of adult from Gulf of Gabes. Above, blackish brown, the black ground color of the neck and fleshy parts sometimes washed with rose and finely spotted with whitish yellow; sides yellowish gray; the brownish black limbs show patches of white at their articulations. Below, the limbs are spotted with whitish yellow. Plastron grayish black flecked with white and yellowish spots (Heldt:1933:13).

Size and Weight. Overall length of juvenile (ex Guinea coast), from tip of snout to terminal tip of carapace, 95 mm.; carapace length approximately 65 mm.; breadth 43 mm.; length of forelimb from axilla to tip 58 mm.

A ♀ killed at Mahfa River mouth was 6 feet long, and 4 feet broad, with an estimated weight of 400 kg. (Büttikofer, 1890: 1:268).

A Luth taken in 1885 on the beach of the Bay of Arzew, measured over 8 feet (2½ metres) long, and 6½ feet (2 metres) broad, according to M. Bouty, Comptroller of Mines, who examined it (Doumergue:1896).

A slightly smaller one taken in the Gulf of Gabes on September 11, 1930, had an *estimated* weight of 650 kg., but this may be exaggerated according to Heldt (1933:9), who should be consulted for measurements of this specimen and more detailed ones of another taken in the Gulf of Gabes on May 27, 1933. Maximum weight has been given as 681.82 kg. (1,500 lbs.) (cf. Deraniyagala, 1939:100).

Breeding. Besides many hundreds of smaller ova, one Luth held 750 eggs with diameters ranging from 10-50 mm., but even the largest were still immature (Heldt:1933). Lays on the Barbary coast (Daudin:1802b). On November 24 and 27 respectively, two Luths came ashore at the mouth of the Mahfa River, Liberia. Hundreds of partially and fully developed eggs were present in the turtle examined by Büttikofer (1890:1:260).

Longevity. Three weeks in New York Aquarium (Flower: 1925).

Parasites. Trematodes (*Astrorchis renicapite* Leidy) of the family Pronocephalidae were present in the intestines of a Gulf of Gabes Luth. Parasites determined by R. P. Dollfus (Heldt: 1933:33).

Companions. A Luth from the Gulf of Gabes was accompanied by about 40 Sucking-fish (*Remora remora*) and 100 Pilot-fish (*Echeneis ductor*) says Heldt (1933: 9 and 31).

Enemies. The flesh, though tough, oily, and an unappetizing red, tasted better than it looked. The abundant green fat was so nearly fluid that it partially melted in Büttikofer's hand. The eggs, though not without an oily taste, were considerably more palatable than the flesh (Büttikofer, 1890:1:268). See also Heldt (1933:35). On the Gold Coast the flesh and eggs are eaten only by the Kru people (Irvine:1947).

Localities. Algeria: Golfe d'Arzeu (Baia d'Arzew). *Tunisia:* Gabes Gulf; Hafacha near Tarf il Ma; Monastir; Sidi Daoud, Cap Bon. *Egypt:* Alexandria market. *East Africa:* Seychelles (no coastal record known to us). *Cape Province:* Algoa Bay; Cape of Good Hope; Table Bay. *Southwest Africa. French*

Equatorial Africa: Gabon. *Togo:* Sebbe (Sebe; Zebe). *Gold Coast:* Tenia (B.M.). *Liberia:* Mahfa River mouth near Robertsport. *French Guinea?:* *"Guinea Coast." *Senegal:* Hann; Rufisque.

Range. All African coasts, Indian and Atlantic Oceans, the Mediterranean and — as an accidental visitor — the temperate seas.

BIBLIOGRAPHY[1]

Works concerning African Cryptodira referred to in the text. For references to generic and specific descriptions see synonymies.

AELLEN, VILLY

1951. Contribution à l'Herpétologie du Maroc. Bull. Soc. Sci. Nat. Maroc, **31**, pp. 153-199, figs. 1 6. (*Not* 1952 as in Zool. Rec.).

AGASSIZ, LOUIS

1857. Contributions to the Natural History of the United States. Boston, 1 and 2, lii + 643 pp., pls. i-xxxiv.

ANDERSON, JOHN

1892. On a Small Collection of Mammals, Reptiles, and Batrachians from Barbary. Proc. Zool. Soc. London, pp. 3-24.

1896. A Contribution to the Herpetology of Arabia, with a Preliminary List of the Reptiles and Batrachians of Egypt. London, pp. 1-122.

1898. Zoology of Egypt, **1**, Reptilia and Batrachia. London, lxvi + 371 pp., figs. 1-14, pls. i-l.

ANDERSSON, L. G.

1903b. (1904) List of Reptiles and Batrachians collected by the Swedish Zoological Expedition to Egypt, the Soudan and the Sinaitic Peninsula. *In* Jägerskiöld, L. A., Results of the Swedish Zoological Expedition to Egypt and the White Nile 1901, **1**, No. 4, pp. 1-12 (This separate appeared in 1903, *fide* wrapper).

1937. Reptiles and Batrachians collected in the Gambia by Gustav Svensson and Birger Rudebeck (Swedish Expedition 1931). Arkiv Zool., **29A**, No. 16, pp. 1-28, figs. 1-8.

ANGEL, FERNAND

1937b. Sur la Faune herpétologique de l'Archipel du Cap-Vert. Comptes Rendus XII. Congrès Internat. Zool. Lisbonne 1935, 3, pp. 1693 1700.

[1] Where a date is followed by a letter of the alphabet, it indicates that during the year cited the author in question published more than one paper on African herpetology. The letter has chronological significance in a more comprehensive bibliography of African herpetology (1880-1955) which it is hoped may be published in the not-too-distant future.

1941a. Sur la Présence à Madagascar de Tortues du Genre *Kinixys* Bull. Mus. Hist. Nat. (Paris), (2), **13**, pp. 151-152.

Angel, F., and H. Lhote

1938. Reptiles et Amphibiens du Sahara central et du Soudan. Bull. Com. Études Hist. Sci. Afr. Occid. Franc., **21**, pp. 345-384.

Ansorge, J. W.

1899. Under the African Sun. New York, pp. 1-355, 134 text illus.; 2 col. pls.

Archer, W. H.

1948a. The Mountain Tortoise (*Geochelone pardalis*). African Wild Life (Johannesburg), **2**, No. 2, pp. 74-77, photos.

1948b. The Mountain Tortoise (*Geochelone pardalis*). African Wild Life (Johannesburg), **2**, No. 3, pp. 75-78, photos.

Astre, Gaston

1948. Reproduction de la Tortue mauresque à Toulouse. Bull. Soc. Hist. Nat. Toulouse, **83**, pp. 60-64.

Aubusson, Louis Magau D'

1894. Esquisse de la Faune egyptienne. Bull. Inst. Egypt, **4**, pp. 217-
(1893) 238, 293-314 (5.v.1893).

Aurelio Basilio, R. P.

1952. La Vida Animal en la Guinea Espanola. (Inst. Estudios Africanos: Madrid), xii + 146 pp., pls.

Babcock, H. L.

1930. Variations in the Number of Costal Shields in *Caretta*. Amer. Nat., **64**, pp. 95-96.

Bailly-Maitre, (M.)

1928. Une jeune Tortue d'Algérie vivante . . . à Narbonne. Bull. Soc. Nat. d'Acclimat. France, **75**, pp. 111-112.

Baker, S. W.

1867. The Nile Tributaries of Abyssinia. Philadelphia, xxiv + 575 pp., photo, illus., maps.

Bally, P. R. O.

1946. Tortoises Eating Bones. Jour. East Afr. Uganda Nat. Hist. Soc.,
(1945) **18**, p. 163.

1952. Einige Beobachtungen an der ostafrikanischen Pantherschildkröte, *Testudo pardalis*. Zool. Garten (Leipzig), **19**, pp. 236-238.

Barbier, H.

1905. Les Cheloniens du Musée d'Histoire Naturelle d'Elbeuf. Bull. Soc. Étude Sci. Nat. Elbeuf, **23**, pp. 68-102, pls. iii-iv.

1907. Les Crocodiliens et les Batraciens du Musée d'Histoire Naturelle d'Elbeuf. Bull. Soc. Étude Sci. Nat. Elbeuf, **25**, pp. 35-74.

Barbour, T., and A. Loveridge

1930a. Reptiles and Amphibians from Liberia. *In* Strong, Richard, Report of the Harvard-African Expedition upon the African Republic of Liberia and the Belgian Congo. Cambridge, **2**, pp. 786-796.

Bateman, G. C.

1897. The Vivarium. London, pp. 1-424, figs. 1-98; pl.

Battersby, J. C.

1954. Reptiles and Amphibians collected in the Northern Frontier Division of Kenya in 1951. Ann. Mag. Nat. Hist., (12), **7**, pp. 241-248.

Baur, Georg

1892. Bemerkungen über verschiedene Arten von Schildkröten. Zool. Anz., **15**, pp. 155-159.

1893. Notes on the Classification and Taxonomy of the Testudinata. Proc. Amer. Philos. Soc., **31**, pp. 210-225.

Bechstein, J. M.

1800. *In* Lacépède, B. G. E. de "Naturgeschichte der Amphibien . . . und der Schlangen . . ." **1**, xxxii + 524 pp., col. pls. i-xxvii.

Bedriaga, J. V.

1882. Die Amphibien und Reptilien Griechenlands. Bull. Soc. Imp.
(1881) Nat. Moscou, **56**: pt. 2, pp. 278-344.

Bell, Thomas

1827. On Two New Genera of Land Tortoises. Trans. Linn. Soc. London, **15**, pp. 392-401, pls. xvi-xvii.

1828a. Descriptions of Three New Species of Land Tortoises. Zool. Jour., **3**, pp. 419-421, (pls. xxiii-xxv in Supplement).

1828b. Characters of the Order, Families, and Genera of the Testudinata. Zool. Jour., **3**, pp. 513-516.

1836-1842. A Monograph of the Testudinata. London, xxiv + 80 unnumbered pages accompanying 40 unnumbered col. pls.

Bernstein, R. E.

1938. Blood Cytology of the Tortoise, *Testudo geometrica*. S. Afr. Jour Sci., **35**, pp. 327-331, fig.

Berthold, A. A.

1850. Über *Cinixys homeana* Bell. Nova Act. Acad. Leopold-Carol. (Bonn), **22**, pp. 423-428, pls. xliii-xlv.

Bianconi, J. J.

1847-1862. Specimina zoologica mosambicana. Bononiae, pp. 1-282, pls. i-xvii (reprints of a series of articles from Mem. Accad. Sci. Ist. Bologna).

Blanford, W. T.

1870. Observations on the Geology and Zoology of Abyssinia, made during the Progress of the British Expedition to that Country. London, xii + 487 pp., figs., pls. i-viii + i-iv.

Blumenbach, J. F.

1804. Abbildungen naturhistorischer Gegenstände. Text unpaged, 100 illus. (the pertinent ones — nos. 66-70 — were published in 1804).

Bocage, J. V. Barboza du

1866a. Lista dos Reptis das Possessões portuguezas d'Africa Occidental que existem no Museu de Lisboa. Jorn. Sci. Lisboa, **1**, pp. 37-56.

1867a. Segunda Lista dos Reptis das Possessões portuguezas d'Africa Occidental que existem no Museu de Lisboa. Jorn. Sci. Lisboa, **1**, pp. 217-228.

1887a. Mélanges erpétologiques. Jorn. Sci. Lisboa, **11**, pp. 177-211.

1887b. (Merely a postscript to a paper on birds.) Jorn. Sci. Lisboa, **12**, p. 86.

1895a. Herpétologie d'Angola et du Congo. Lisbon, xx + 203 pp., pls. i-xix.

1896a. Reptis de algumas Possessões portuguezas d'Africa que existem no Museu de Lisboa. Jorn. Sci. Lisboa, (2), **4**, pp. 65-104.

1902. Avis e Reptis de Cabo Verde. Jorn. Sci. Lisboa, (2), **6**, pp. 206-210.

1903a. Contribution à la Faune des quatres Îles du Golfe de Guinée. Jorn. Sci. Lisboa, (2), **7**, pp. 25-59.

Boettger, Oskar

1874. Reptilien von Marocco und von den canarischen Inseln. Abhandl. (1873) Senckenberg. Naturf. Ges., **9**, pp. 121-192, pl.

1880. Die Reptilien und Amphibien von Syrien, Palaestina und Cypern. Ber. Senckenberg. Naturf. Ges., pp. 132-220, pls. iii-iv.

1883a. Die Reptilien und Amphibien von Marocco II. Abhandl. Senckenberg. Naturf. Ges., **13**, pp. 93-146, pl.

1885a. Materialien zur Fauna des unteren Congo I. Ber. Offenbach. Ver. Naturk., **24-25**, pp. 171-186.

1885b. Liste der von Hrn. Dr. med. W. Kobelt in Algerien und Tunisien gesammelten Kriechtiere. *In* Kobelt, W., Reiseerinnerungen aus Algerien und Tunis. Frankfurt a. M., pp. 457-475.

1887b. Zweiter Beitrag zur Herpetologie Südwest- und Süd-Afrikas. Ber. Senckenberg. Naturf. Ges., pp. 135-173, pl. v.

1888a. Materialien zur Fauna des unteren Congo II. Ber. Senckenberg. Naturf. Ges., pp. 3-108, pls. i-ii.

1889. Herpetologische Miscellen. Ber. Senckenberg. Naturf. Ges., pp. 267-316.

1893a. Katalog der Reptilien-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main. Frankfurt a. M., ix + 140 pp.

1893b. Übersicht der von Prof. C. Keller anlässlich der Ruspoli'schen Expedition nach den Somaliländern gesammelten Reptilien und Batrachier. Zool. Anz., **16**, pp. 113-119, 129-132.

1894a. Aufzählung der Arten. *In* Dr. Eduard Fleck's Reiseausbeute aus Südwest-Afrika. Ber. Senckenberg. Naturf. Ges., pp. 88-93.

1913. Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas. (Sammlung Voeltzkow 1889-1895 u. 1903-1905). *In* Voeltzkow, A., 1908-1917, Reise in Ostafrika. Stuttgart, **3**, pp. 269-376, pls. xxiii-xxx.

BOETTGER, OSKAR, and GUSTAV TORNIER

1900. Eine ornithologische Forschungsreise durch Tunesien. Zweiter (1899) Teil, kurzer Reisebericht. Jour. für Ornith., pp. 63-65.

BOJANUS, L. H.

1819-1821. Anatome Testudinis Europaeae . . . Vilnae, vi + 178 pp., figs. 1-201, pls. i-xxxix.

BONAPARTE, C. L.

1831. Saggio di una Distribuzione metodica degli Animali Vertebrati. Rome, pp. 1-144.

BONNATERRE, ABBÉ

1789. Erpétologie, *In* Tableau encyclopedique et méthodique des trois Règnes de la Nature. Paris, xxviii + 70 pp., pls. A + i-xlii.

BORY DE ST. VINCENT, J. B. G. M.

1828. Resumé d'Erpétologie ou d'Histoire naturelle des Reptiles. Paris, vii + 292 pp.

1829. Iconographie des Reptiles. Paris, pp. 1-20, pls. i-lii.

BOULENGER, E. G.

1920b. Exhibition of, and Remarks on, Living Specimens of a Remarkable New Land-Tortoise (*Testudo loveridgii*). Proc. Zool. Soc. London, p. 190.

BOULENGER, G. A.

1886b. On the South-African Tortoises Allied to *Testudo geometrica*. Proc. Zool. Soc. London, pp. 540-542, pls. lvii-lviii.

1888d. On New and Little-known South-African Reptiles. Ann. Mag. Nat. Hist., (6), **2**, pp. 136-141.

1888g. Description of a New Land-Tortoise from South Africa from a Specimen Living in the Society's Gardens. Proc. Zool. Soc. London, p. 251, pl. xiv.

1889a. Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History). London, ix + 311 pp., figs. 1-73, pls. i-vi.

1889b. On the Reptiles and Batrachians Obtained in Morocco by M. Henry Vaucher. Ann. Mag. Nat. Hist., (6), **3**, pp. 303-307.

1890f. Notes on the Secondary Sexual Characters in the South-African Tortoises of the Genus *Homopus*. Proc. Zool. Soc. London, p. 521.

1891c. Catalogue of the Reptiles and Batrachians of Barbary (Morocco, Algeria, Tunisia), Based Chiefly upon the Notes and Collections made in 1880-1884 by M. Fernand Lataste. Trans. Zool. Soc. London, **13**, pp. 93-164, pls. xiii-xviii.

1896a. A List of the Reptiles and Batrachians Collected by Dr. Ragazzi in Shoa and Eritrea. Ann. Mus. Civ. Stor. Nat. Genova, (2), **16**, pp. 545-554.

1896c. Report on Capt. Bottego's Second Collection of Reptiles and Batrachians from Somaliland. Ann. Mus. Civ. Stor. Nat. Genova (2), **17**, pp. 15-23.

1897g. A List of the Reptiles and Batrachians of Somaliland and Gallaland. Ann. Mus. Civ. Stor. Nat. Genova, (2), **17**, pp. 275-280.

1898a. Concluding Report on the Late Capt. Bottego's Collection of Reptiles and Batrachians from Somaliland and British East Africa. Ann. Mus. Civ. Stor. Nat. Genova, (2), **18**, pp. 715-723, pls. ix-x.

1900b. A List of the Batrachians and Reptiles of the Gaboon (French Congo), with Descriptions of New Genera and Species. Proc. Zool. Soc. London, pp. 433-456, figs. 1-2, pls. xxvii-xxxii.

1902b. A List of the Fishes, Batrachians, and Reptiles Collected by Mr. J. ffolliott Darling in Mashonaland, with Descriptions of New Species. Proc. Zool. Soc. London, **2**, pp. 13-18, pls. ii-iv.

1902d. List of the Cold-blooded Vertebrates Hitherto Recorded from the Uganda Protectorate. An appendix to Johnston, H. H., The Uganda Protectorate. London, **1**, pp. 445-447.

1903a. The Reptiles of Sokotra. *In* Forbes, H. O., The Natural History of Sokotra and Abd-el-kuri. Liverpool, pp. 75-96, pls. viii-xi.

1903e. On a Collection of Batrachians and Reptiles from the Interior of Cape Colony. Ann. Mag. Nat. Hist., (7), **12**, pp. 215-217, pls. xvi-xvii.

1905f. Reptiles de la Guinée espagnole. Mem. Real Soc. Esp. Hist. Nat. (Madrid), **1**, pp. 183-186.

1905h. On a Collection of Batrachians and Reptiles made in South Africa by Mr. C. H. B. Grant, and Presented to the British Museum by Mr. C. D. Rudd. Proc. Zool. Soc. London, pp. 248-255.

1906i. Report on the Reptiles Collected by the late L. Fea in West Africa. Ann. Mus. Civ. Stor. Nat. Genova, (3), **2**, pp. 196-216, figs. 1-9.

1907a. On a Collection of Fishes, Batrachians, and Reptiles, made by Mr. S. A. Neave in Rhodesia, North of the Zambesi, with Field Notes by the Collector. Mem. Proc. Lit. Philos. Soc. Manchester, **51**, pp. 1-12.

1907j. Second Report on the Reptiles and Batrachians Collected in South Africa by Mr. C. H. B. Grant, and Presented to the British Museum by Mr. C. D. Rudd. Proc. Zool. Soc. London, pp. 478-487, figs. 140-141, pls. xxi-xxii.

1911c. On a Third Collection of Reptiles and Batrachians Made by Dr. E. Bayon in Uganda. Ann. Mus. Civ. Stor. Nat. Genova, (3), **5**, pp. 161-169.

1912b. Missione per la Frontiere Italo-Etiopica sotto il Comando del Capitano Carlo Citerni. Resultati zoologici. List of the Reptiles and Batrachians. Ann. Mus. Civ. Stor. Nat. Genova, (3), **5**, pp. 329-332.

1919g. Batraciens et Reptiles recueillis par le Dr. C. Christy au Congo belge dans les Districts de Stanleyville Haute-Uelé et Ituri en 1912-1914. Revue Zool. Afr., **7**, pp. 1-29.

1920e. Une Tortue extraordinaire: *Testudo Loveridgii*, sp. n. Comptes Rendus Acad. Sci. (Paris), **170**, pp. 263-266.

1920d. Présidence de Mm. Boulenger, Président d'honneur et Rabaud Vice-Président. Bull. Soc. Zool. France, **45**, pp. 58-69.

Bowker, F.

1926. Tortoise Eggs and Nests. S. Afr. Jour. Nat. Hist., **6**, p. 37.

Braestrup, F. W.

1947. Remarks on Faunal Exchange through the Sahara. Vidensk. Medd. Dansk. Naturh. Foren, **110**, pp. 1-15, fig. 1.

Brühl, C. B.

1874-1882. Zootomie aller Thierklassen für Lernende nach Autopsien skizzirt. Wien, pls. i-civ.

Burton, Maurice

1953. Tortoise Tango and Dog Dance. Illus. London News, 4.vii.53, p. 34, fig., photo.

Büttikofer, Johannes

1890. Reisebilder aus Liberia. Leiden, **1** and **2**, pp. 1-510, figs., pls. i-xxxii.

Buxton, R. D.

1937. A Natural History of the Turkana Fauna. Jour. E. Afr. Uganda (1936) Nat. Hist. Soc., **13**, pp. 85-104, pls. A-H + i-vi.

Cadenat, Jean

1949. Notes sur les Tortues marines des Côtes du Senegal. Bull. Inst. Franc. Afrique Noire, **11**, pp. 16-35, figs. 1-18.

Cairncross, B. L.

1946. Notes on South African Tortoises. Ann. Transvaal Mus., **20**, pp. 395-397, pl. i.

Calabresi, Enrica

1916. Batraci e Rettili raccolti nella Somalia meridionale dai Dott.

Stefani e Paoli. Monitore Zool. Ital. (Firenze), **27**, pp. 33-45, pl. ii.

1923a. Missione Zoologica del Dr. E. Festa in Cirenaica. Boll. Mus. Zool. Anat. Comp. Univ. Torino, **38**, No. 7, pp. 1-28.

1927. Anfibi e Rettili raccolti nella Somalia dai Proff. G. Stefanini e N. Puccioni. Atti. Soc. Ital. Sci. Nat. (Milano), **66**, pp. 14-60, pl. i.

CAMERANO, LORENZO

1877. Dei Caratteri Sessuali Secondari della *Testuda ibera* Pallas. Atti Real Accad. Sci. Torino, **13**, pp. 97-102, pl. iv.

CANSDALE, G. S.

1948c. Reptile Collecting in West Africa. II. Crocodiles, Turtles and Snakes. Scottish Zoo and Wild Life (Edinburgh), **1**, pp. 70-78, pl.

1955. Reptiles of West Africa. Penguin Books: London, pp. 1-104, figs. A-H.

CARPENTER, G. D. H.

1920. A Naturalist on Lake Victoria. London, xxiv + 333 pp., figs., pls. i-ii, map (chapter IX. Reptiles, etc.).

CARR, ARCHIE

1952. Handbook of Turtles. The Turtles of the United States, Canada and Baja California. Ithaca, N. Y., xv + 542 pp., figs. 1-37, pls. i-lxxxii.

CERF, F. LE

1907. Reptiles et Batraciens observés à Maison-Carée (Algerie). Ann. Assoc. Natur. Levallois-Perret, **13**, pp. 22-26.

CHABANAUD, PAUL

1916c. Sur divers Reptiles et Batraciens du Maroc recueillis par M. Pallary. Bull. Mus. Hist. Nat. (Paris), **22**, pp. 228-233, figs. 1-2.

1917c. Énumération des Reptiles non encore étudiés de l'Afrique occidentale, appartenant aux Collections du Museum, avec la Description des Espèces nouvelles. Bull. Mus. Hist. Nat. (Paris), **23**, pp. 83-105, figs. 1-13.

1921a. Contribution à l'Étude de la Faune herpétologique de l'Afrique occidentale. Deuxième Note. Bull. Com. Études Hist. Sci. Occ. Franç. (Paris), pp. 445-472, pls. i-iv, map.

1921b. Mission Paul Chabanaud en Afrique occidentale (1919-1920). Liste des Batraciens et des Reptiles. Bull. Mus. Hist. Nat. (Paris), **27**, pp. 519-525.

CHAIGNON, H. DE

1904. Contributions à l'Histoire naturelle de la Tunisie. Bull. Soc. Hist. Nat. Autun, **17**, pp. 1-166.

CHUBB, E. C.
1908. List of Batrachia and Reptilia collected in Northern Matabele land. Ann. Mag. Nat. Hist., (8), **2**, pp. 218-221.
1909a. The Batrachians and Reptiles of Matabeleland. Proc. Zool. Soc. London, pp. 590-597.
1909b. List of Rhodesian Batrachians and Reptiles in the Rhodesia Museum Collection. Rhodesia Mus., Bulawayo, Ann. Rep., **8**, pp. 34-36.

CONANT, ROGER, and ALEXANDER DOWNS
1940. Miscellaneous Notes on the Eggs and Young of Reptiles. Zoologica (New York), **25**, pp. 33-48.

CONANT, ROGER, and R. G. HUDSON
1949. Longevity Records for Reptiles and Amphibians in the Philadelphia Zoological Garden. Herpetologica (San Diego), **5**, pp. 1-8.

COOPER, B.
1948. Note on a Land Tortoise. Ann. Rep. Game Pres. Dept. Tanganyika Territory, 1947, p. 11.

COPE, E. D.
1859. Notes and Descriptions of Foreign Reptiles. Proc. Acad. Nat.
(1860) Sci. Philadelphia, pp. 294-297.

COTT, H. B.
1928. Report on the Zoological Society's Expedition on the Zambesi, 1927. Proc. Zool. Soc. London, pp. 923-961, pls. i-iv.

COZZOLINO, A.
1938. Osservazioni etologiche sulla *Chelone mydas* delle Coste Somalia italiana. Riv. Biol. Colon., **1**, pp. 241-248, graph.

CUVIER, G. L. C. F. D.
1817. La Règne Animal distribué d'après son Organisation, pour servir de base à l'Histoire naturelle des Animaux et d'Introduction à l'Anatomie comparée. ed. 1, Paris: Deterville, **2**, Les Reptiles . . ., xviii + 532 pp.
1829. La Règne Animal . . . ed. 2, Paris, Deterville, **2**, Les Reptiles . . ., xvi + 406 pp.
1838. La Règne Animal . . . ed. 3, Paris, Fortin, Masson et Cie, **3**, Les Reptiles avec un Atlas par M. Duvernoy, pp. 1-169, pls. i-xlii.

DAUBENTON, E. L.
1784. Les Animaux Quadrupèdes ovipares et Les Serpents. *In* Encyclopédie méthodique, **2**, pp. 545-712.

DAUDIN, F. M.
1802. Histoire naturelle, générale et particulière, des Reptiles. Paris, **2**, pp. 1-432, pls. xvi-xxviii.

DERANIYAGALA, P. E. P.
1939. The Tetrapod Reptiles of Ceylon. I. Testudinates and Crocodilians. xxxii + 412 pp., figs. 1-137, pls. i-xxiv.

1943. Subspecies Formation in Loggerhead Turtles (Carettidae). Spolia Zeylanica (Colombo), **23**, pp. 79-92, figs. 1-7.

1948. Some Scientific Results of two Visits to Africa. Spolia Zeylanica, **25**, Pt. 2, pp. 1-42, pls. i-xiv.

DOLLFUS, R. P.

1929 Notules herpétologiques marocaines. Bull. Soc. Sci. Nat. Maroc (Rabat), **9**, p. 112.

DOUMERGUE, F.

1896. Contributions à la Faune erpétologique de la Province d'Oran. Compte Rendu Assoc. Franc. Avanc. Sci., Carthage, **25**, pt. 2, pp. 477-478.

1899. Essai sur la Faune erpétologique de l'Oranie. Soc. Géogr. Arch. Oran, **19**, pp. 197-260, 501-532, pls. i-v.

DUERDEN, J. E.

1906a. How the Berg-Schilpad Lays her Eggs. (Published in local paper of Feb. 2 as Albany Mus. Notes, XIII. Not seen.)

1906c. South African Tortoises of the Genus *Homopus*, with Description of a New Species. Rec. Albany Mus., **1**, pp. 405-411, figs. 1-6, pl. xi. (Actually the description of *boulengeri* was first published in local paper of May 5 as Albany Mus. Notes, XVIII.)

1907a. Report of the Albany Museum for 1906. Pp. 9-10. (A simple list of species together with localities which are apparently the donors' addresses and not necessarily the place of origin.)

1907b. Genetics of the Colour Pattern in Tortoises of the Genus *Homopus* and its Allies. Rec. Albany Mus., **2**, pp. 65-92, figs. 1-9, pls. vi-viii.

1907c. Variations in the *Geometrica* Group of South African Tortoises.

(1906) Rep. S. Afr. Assoc. Advanc. Sci. for 1905-1906, pp. 178-208.

DUMÉRIL, A. H. A.

1856a. Note sur les Reptiles du Gabon. Revue Mag. Zool., (2), **8**, pp. 369-377, pl. xx.

1860. Reptiles et Poissons de l'Afrique occidentale. Arch. Mus. Hist. Nat. (Paris: 1858-1861), **10**, pp. 137-240, pls. xiii-xix. (The date for this part is 1860, *fide* Roy. Soc. Cat., though frequently cited as 1859 or 1861.)

DUMÉRIL, A. M. C., and G. BIBRON

1835. Erpétologie générale ou Histoire naturelle complète des Reptiles. Paris, **2**, ii + 680 pp., pls. xi-xxiv.

DUMÉRIL, A. M. C., and A. H. A. DUMÉRIL

1851. Catalogue méthodique de la Collection des Reptiles du Museum d'Histoire naturelle de Paris. Paris, iv + 224 pp.

DURRELL, G. M.

1953. The Overloaded Ark. New York, xv + 272 pp., figs.

EADE, PETER
1886. Tortoises. Trans. Norfolk Norwich Nat. Soc., **4**, pp. 316-322.
1893. A further Note upon Tortoises. Trans. Norfolk Norwich Nat. Soc., **5**, pp. 368-372.

EICHWALD, C. E. VON
1851. Naturhistorische Bemerkungen über Algier und den Atlas. Nouv. Mem. Soc. Imp. Nat. Moscou, **9**, pp. 331-464.

ESCHERICH, KARL
1896. Beitrag zur Fauna tunisischen Insel Djerba. Verh. Zool. Bot. Ges. Wien, **46**, pp. 268-279.

EVERSMANN, EDWARD
1854. Einiges aus meinem Tagebuche während einer Reise in's Ausland im Winter 1852-53. Bull. Soc. Imp. Nat. Moscou, **27**, pp. 398-445.

FALK, KURT
1922. Südwestafrikanische Reptilien und ihre Heimat. Wochensch. Aquar.-Terrarienkunde (Braunschweig), **19**, pp. 160-164, figs.

FEJÉRVÁRY, G. J. F. DE
1927. On a Small Collection of Reptiles from Morocco. Ann. Mag. Nat. Hist., (9), **20**, pp. 512-518.

FISK, G. H. R.
1878. Two Leopard Tortoises (*Testudo pardalis*). Proc. Zool. Soc. London, p. 790.

FITZINGER, L. J. F. J. DE
1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften . . . Wien, viii + 66 pp., pl. i.
1835. (1836) Entwurf einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. Ann. Wiener Mus., **1**, pp. 103-128.
1843. Systema Reptilium . . . Fasciculus primus: Amblyglossae (Conspectus geographicus). Vindobonae, pp. 1-106.
1855. Bericht an die kaiserl. Akademie der Wissenschaften über die von dem Herrn. Consulatsverweser Dr. Theodor v. Heuglin für die Menagerie zu Schönbrunn mitgebrachten lebenden Thiere. Sitzungsb. K. Akad. Wiss. Wien, **17**, pp. 242-253.
1861. (1860) Die Ausbeute der österreichischen Naturforscher an Säugethieren und Reptilien während der Weltumsegelung Sr. Majestät Fregatte Novara. Sitzungsb. K. Akad. Wiss. Wien, **42**, pp. 383-416.

FITZSIMONS, V. F.
1932. Preliminary Description of New Forms of South African Reptilia and Amphibia, from the Vernay-Lang Kalahari Expedition, 1930. Ann. Transvaal Mus., **15**, pp. 35-40.
1935a. Notes on a Collection of Reptiles and Amphibians made in the Southern Kalahari, Bushmanland and Great and Little Namaqualand. Ann. Transvaal Mus., **15**, pp. 519-550.

1935b. Scientific Results of the Vernay-Lang Kalahari Expedition, March to September, 1930. Reptilia and Amphibia. Ann. Transvaal Mus., **16**, pp. 295-397, figs. 1-30, pls. x-xi.

1937a. Notes on the Reptiles and Amphibians Collected and Described from South Africa by Andrew Smith. Ann. Transvaal Mus., **17**, pp. 259-274, pl. x.

1938. Transvaal Museum Expedition to South-West Africa and Little Namaqualand, May to August 1937. Reptiles and Batrachians. Ann. Transvaal Mus., **19**, pp. 153-209, pls. ii-iv, map.

1939b. An Account of the Reptiles and Amphibians Collected on an Expedition to South-eastern Rhodesia during December 1937 and January 1938. Ann. Transvaal Mus., **20**, pp. 17 46.

1946a. An Account of the Reptiles and Amphibians Collected on an Expedition to the Cape Province, October to December, 1940. Ann. Transvaal Mus., **20**, pp. 351-377, pls. xiv-xvii.

1950. Notes on a Collection of Reptiles and Amphibians from the West Coast of Southern Africa. Ann. Transvaal Mus., **21**, pp. 253-259, pl. iv.

FLECK, EDOUARD

1894. Vorkommen und Lebensweise der Reptilien und Batrachier. Ber. Senckenberg. Naturf. Ges., pp. 83-87.

FLOWER, S. S.

1900. On some Reptiles and Batrachians from the White Nile. Proc. Zool. Soc. London, pp. 967-968.

1924a. A remarkable Tortoise of the Genus *Testudo*. Proc. Zool. Soc. London, pp. 920-921.

1925b. Contributions to our Knowledge of the Duration of Life in Vertebrate Animals. III. Reptiles. Proc. Zool. Soc. London, pp. 911-981.

1926. Species of Land Tortoises of the Genus *Testudo* Found in the Countries Bordering the Mediterranean Sea. Copeia, p. 133.

1928. Exhibition of a great African Tortoise (*Testudo sulcata*). Proc. Zool. Soc. London, p. 654, figs. 1-2.

1929. Reptiles. *In* List of the Vertebrated Animals exhibited in the Gardens of the Zoological Society of London, 1828-1927. London, **3**, pp. 1-272.

1933. Notes on the Recent Reptiles and Amphibians of Egypt, with a List of the Species Recorded from that Kingdom. Proc. Zool. Soc. London, pp. 745-851, map.

1937a. Further Notes on the Duration of Life in Animals. III. Reptiles. Proc. Zool. Soc. London, pp. 1-39.

1945. Persistent Growth in the Tortoise, *Testudo graeca*, for Thirty-nine Years, with other Notes Concerning that Species. Proc. Zool. Soc. London, **114**, pp. 451-455, fig. 1.

FUCHS, HUGO

1914. Über den Bau und die Entwicklung des Schädels der *Chelone imbricata*. I. Das Primordialskelett des Neurocraniums und Kieferbogens. *In* Voeltzkow, W., Reise in Ostafrika in den Jahren 1903-1905, **5**, pp. 1-325, text figs. 1-182, pls. i-iv.

GADOW, HANS

1901. Amphibia and Reptiles. *In* The Cambridge Natural History. London, **8**, xiii + 668 pp., figs. 1-181, map (reprinted in 1920).

GENDRE, E.

1909. Liste de quelques Espèces de Reptiles du Fouta Djalon. Comptes Rendus Soc. Linn. Bordeaux, **63**, pp. cv-cvi.

GEOFFROY ST.-HILAIRE, E. F.

1809a. Sur les Tortues molles, nouveau genre sous le Nom de *Trionyx* et sur la Formation des Carapaces. Ann. Mus. Hist. Nat. (Paris), **14**, pp. 1-20, pls. i-v.

1809b. Synopsis of 1809a. Nouv. Bull. Soc. Philom. Paris, **22**, pp. 363-367.

1827a. Description des Reptiles qui se trouvent en Égypte. *In* Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée Française (1798-1801), **1**, Histoire naturelle. Paris, pp. 115-184, pls. i-vi.

GERVAIS, F. L. P.

1836. Énumération de quelques Espèces de Reptiles provenant du Barbarie. Ann. Sci. Nat. Zool. (Paris), (2), **6**, pp. 308-313.

1848. Sur les Animaux vértebrés de l'Algérie. Ann. Sci. Nat. Zool. (Paris), (3), **10**, pp. 202-208.

1872. Ostéologie du Sphargis Luth (*Sphargis coriacea*). Arch. Mus. Hist. Nat. (Paris), (N.S.), **8**, pp. 199-228, pls. v-ix.

GESTRO, RAFFAELE and DECIO VINCIGUERRA

1931. Rettili, Batraci. *In* Resultati scientifici della Missione alla Oasi di Giarubub. 1926-1927. Roma, **4**, pp. 538-539. (This is a reprint, but under two names, of Vinciguerra's 1927 paper in Ann. Mus. Civ. Stor. Nat. Genova).

GHIGI, ALESSANDRO

1913. Materiali per lo Studio della Fauna Libica. Mem. Accad. Sci. Inst. Bologna, (6), **10**, pp. 253-296.

1932. Escursione zoologica all Oasi di Marrakesch nell' Aprile 1930. Boll. Zool. (Napoli), **3**, pp. 197-208.

GIRONS, H. SAINT

1953c. Influence de la Mise en Eau du Barrage de Bin el Ouidane sur les Vertébrés terrestres. Bull. Soc. Sci. Nat. Maroc, **33**, pp. 75-80, figs. 1-2.

GMELIN, J. F.

1789. Caroli a Linné . . . Systema Naturae . . . (ed. 13, Lipsiae), 1. (1788) part 3, pp. 1033-1516 (Date of this part is 1789, *fide* John Hopkinson, 1907, Proc. Zool. Soc. London, pp. 1035-1037).

GOLDFUSS, G. A.

1820. Handbuch der Zoologie. Nürnberg, **2**, pp. 1-510, pls. iii-iv.

GORHAM, F. W. and A. C. IVY

1938. General Function of the Gall Bladder from the Evolutionary Standpoint. Field Mus. Nat. Hist., Zool. Ser., **22**, pp. 159-213.

GRAY, J. E.[1]

1825. A Synopsis of the Genera of Reptiles and Amphibia, with a Description of Some New Species. Ann. Philos., (2), **10**, pp. 193-217.

1828 and 1830. Specilegia Zoologica; or Original Figures and Short Systematic Descriptions of New and Unfigured Animals. Part I (1828), pt. II (1830), pp. 1-12 (pls. i-ix were never issued but an unpublished set of them is in the Brit. Mus.).

1831b. Synopsis of the Species of the Class Reptilia. *In* Griffith, E., The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier. London, **9**, pp. 1-481 + 1-110, pls. i-xlii (Gray is on pp. 1-110 of addenda. In his Bibliography the date of this work appears as 1830, possibly an earlier printing. It seems to have come out before 1831c which is usually cited for the fuller descriptions of new names).

1831c. Synopsis Reptilium or Short Descriptions of the Species of Reptiles. Part I. Cataphracta, Tortoises, Crocodiles, and Enaliosaurians. London, viii + 85 pp., pls. i-xi.

1844. Catalogue of the Tortoises, Crocodiles, and Amphisbaenians, in the Collection of the British Museum. London, pp. 1-80.

1854. (1852) Descriptions of a New Genus and Some New Species of Tortoises. Proc. Zool. Soc. London, for 1852, pp. 133-135.

1855. Catalogue of Shield Reptiles in the Collection of the British Museum. I. Testudinata (Tortoises). London, pp. 1-82, pls. i-xlii.

1856. (1855) On Some New Species of Freshwater Tortoises from North America, Ceylon and Australia, in the Collection of the British Museum. Proc. Zool. Soc. London, for 1855, pp. 197-202.

1860a. Description of a Soft Tortoise (*Aspidochelys Livingstonii*) from the Zambesi, Sent to the British Museum by Dr. Livingstone. Proc. Zool. Soc. London, pp. 5-6, pl. xxii.

[1] Despite its numerous inaccuracies and errors, we have been greatly helped in assembling this list of Gray's publications on African testudinates by a "List of the Books, Memoirs and Miscellaneous Papers by John Edward Gray." Compiled in 1874-1875 by J. Saunders, London. Privately printed pamphlet listing about 1,162 titles.

1860b. Description of a New Species of *Emys* Lately Living in the Gardens of the Zoological Society. Ann. Mag. Nat. Hist., (3), **6**, pp. 148-149.

1860c. Reprint of 1860b. Proc. Zool. Soc. London, pp. 232-233, pl. xxx.

1860d. On the African Trionices with Hidden Feet (*Emyda*). Ann. Mag. Nat. Hist., (3), **6**, pp. 440-442.

1860e. Reprint of 1860d. Proc. Zool. Soc. London, pp. 314-316.

1860f. Note on *Aspidochelys Livingstonii*. Proc. Zool. Soc. London, pp. 430-431.

1861. Reprint of 1860f. Ann. Mag. Nat. Hist., (3), **7**, pp. 226-227.

1863b. Notice of a New Species of *Kinixys* and Other Tortoises from Central Africa. Ann. Mag. Nat. Hist., (3), **12**, pp. 381-382.

1863f. On the Species of the Genus *Sternothaerus*, with some Observations on *Kinixys*. Proc. Zool. Soc. London, pp. 192-197, figs.

1864a. Reprint of 1863f. Ann. Mag. Nat. Hist., (3), **13**, pp. 165-170.

1864c. Revision of the Species of Trionychidae found in Asia and Africa, with the Descriptions of Some New Species. Proc. Zool. Soc. London, pp. 76-98, figs. 1-21.

1864d. On the Genera of Chelydidae and the Characters Furnished by the Study of their Skulls. Proc. Zool. Soc. London, pp. 128-135, figs. 1-3.

1865d. Notes of a New Genus and Species of the Family Trionychidae from West Africa. Ann. Mag. Nat. Hist., (3), **16**, pp. 204-206, fig.

1865e. Reprint of 1865d. Proc. Zool. Soc. London, pp. 323-325, fig.

1865f. On the Development of the Sternal Callosities in *Cyclanosteus senegalensis*, and on the Synonyms of *Cyclanosteus* and its Allied Genera. Proc. Zool. Soc. London, pp. 422-428, figs. 1-2.

1866. Notes on some Young Specimens of Tortoises (*Testudo*). Proc. Zool. Soc. London, pp. 305-306.

1869b. Descriptions of a New Species of Freshwater Turtle and Chameleon. *In* Petherick, John, Travels in Central Africa and Explorations of the western Nile Tributaries. London, **2**, Appendix B, pp. 189-193.

1869c. Notes on the Families and Genera of Tortoises (Testudinata), and on the Characters Afforded by the Study of their Skulls. Proc. Zool. Soc. London, pp. 165-225, figs. 1-20, pl. xv. (incorporated in 1870e with very few changes).

1869d. Description of *Mauremys laniaria*, a new Freshwater Tortoise. Proc. Zool. Soc. London, pp. 499-500, pl. xxxvii.

1869e. Descriptions of *Emys flavipes*. Proc. Zool. Soc. London, pp. 643-644, pl. 1 (i.e. 50).

1870c. Notes on Tortoises in the British Museum, with Descriptions of Some New Species. Proc. Zool. Soc. London, pp. 653-659, pls. xxxiii-xxxiv.

1870d. Notes on a Specimen of *Cyclanosteus senegalensis* Living in the Society's Gardens. Proc. Zool. Soc. London, pp. 717-718, pl. xliii.

1870e. Supplement to the Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata (Tortoises). London, ix + 120 pp., figs. 1-40.

1872b. Letterpress to Sowerby and Lear, Tortoises, Terrapins, and Turtles. London, pp. 1-16, pls. i-lx. (Two-thirds of these plates previously appeared in Bell, 1825, Monograph of the Tortoises, which was never completed.) See also Gray's remarks in 1872, Ann. Mag. Nat. Hist., (4), **10**, p. 407.

1872c. Appendix to the Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata. London, pp. 1-28.

1873. Notes on the Mud-Tortoises (*Trionyx*, Geoffroy) and on the Skulls of the Different Kinds. Proc. Zool. Soc. London, pp. 38-72, figs. 1-10, pl. viii.

1873b. Hand-List of the Specimens of Shield Reptiles in the British Museum. London, pp. 1-124.

1873c. On the Skulls and Alveolar Surfaces of Land-Tortoises (Testudinata). Proc. Zool. Soc. London, pp. 722-728, pl. lx.

1873d. Notes on Tortoises. Ann. Mag. Nat. Hist., (4), **11**, pp. 143-149.

1873e. On the Original Form, Development, and Cohesion of the Bones of the Sternum of Chelonians, with Notes on the Skeleton of *Sphargis*. Ann. Mag. Nat. Hist., (4), **11**, pp. 161-172, pls. iv-vi.

1873f. Observations on Chelonians, with Descriptions of New Genera and Species. Ann. Mag. Nat. Hist., (4), **11**, pp. 289-308.

1873g. On an Adult Skeleton of *Tyrse nilotica* in the British Museum. Ann. Mag. Nat. Hist., (4), **11**, pp. 470-471.

1873h. Additional Notes on the Form of the Bones in the Sternum of Very Young Tortoises, and their Development. Ann. Mag. Nat. Hist., (4), **12**, pp. 319-322, pl. xii.

1873i. On a Variety of *Chersine angulata*. Ann. Mag. Nat. Hist., (4), **12**, p. 496.

1873j. Notes on the Genera of Turtles (*Oiacopodes*), and Especially on their Skeletons and Skulls. Proc. Zool. Soc. London, pp. 395-411, figs. 1-3.

GRAVENHORST, J. L. C.

1829. Reptilia Musei zoologici Vratislaviensis recensita et descripta . . . Part I. Chelonios et Batrachia. Del. Musei zool. Vratislaviensis, **1**, xiv + 106 pp., pls. i-xvii.

GREEF, S. R.

1885. Ueber die Fauna der Guinea-Inseln S. Thomé und Rolas.

(1884) Sitzungsb. Ges. Bedförd. Naturw. Marburg, 1884, pp. 41-80.

GRIFFINI, ACHILLE

1911. Le Testuggini gigantesche. Boll. Matemat. Sci. Fis. Natur., **13**, pp. 3-7 (? reprint pagination).

GRIFFITH, EDWARD

1831. The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier. London, **9**, Reptilia, 481 + 110 pp. (latter solely Synopsis by Gray), pls. i-xlii.

GÜNTHER, ALBERT

1869a. Report on Two Collections of Indian Reptiles. Proc. Zool. Soc. London, pp. 500-507, figs. 1-4, pls. xxxviii-xl.

1869b. Reptilia. Zool. Record, **6**, pp. 105-122.

1894a. Second Report on the Reptiles, Batrachians, and Fishes trans-
(1893) mitted by Mr. H. H. Johnston, C. B., from British Central Africa. Proc. Zool. Soc. London, pp. 616-628, pls. liii-lvii.

1894c. Report on the Collection of Reptiles and Fishes made by Dr. J. W. Gregory during his Expedition to Mount Kenia. Proc. Zool. Soc. London, pp. 84-88, pl. viii.

1896. Report on a Collection of Reptiles and Fishes made by Miss M. H. Kingsley During her Travels on the Ogowe River and in Old Calabar. Ann. Mag. Nat. Hist., (6), **17**, pp. 261-285.

GUÉRIN, MÉNEVILLE (F. E. GUÉRIN-MÉNEVILLE)

1829-
1841. Iconographie de Règne Animal de G. Cuvier, ou représentation d'aprés Nature de l'une des Espèces les plus remarquables, et souvent non encore figurés de chaque Genre d'Animaux. Avec un Text descriptif, etc. Paris and London, **1**, pls. i-xxx, **3**, xvi + 576 pp.

GUICHENOT, ALPHONSE

1850. Histoire naturelle des Reptiles et des Poissons, *In* Exploration scientifique de l'Algérie pendant les Années 1840, 1841, 1842. Sci. Phys. Zool. Paris, **5**, iv + 144 pp., pls. i-iv + i-viii.

1851. Reptiles. *In* Lefebvre, Théophile, Voyage en Abyssinie exécuté pendant les Années 1839, 1840, 1841, 1842, 1843 par une Commission scientifique . . . Part 4, Hist. nat.-zool. Paris, **6**, pp. 1-398, pls. i-iv.

HALLOWELL, EDWARD

1839. Description of a Species of Land Tortoise from Africa. Jour. Acad. Nat. Sci. Philadelphia, **8**, pp. 161-189, pls. viii-ix.

1844. Description of New Species of Reptiles from Africa. Proc. Acad. Nat. Sci. Philadelphia, pp. 118-120.

HAMERTON, A. E.

1933. Report on Deaths occurring in the Society's Gardens during the year 1932. Proc. Zool. Soc. London, pp. 451-482, pls. i-iii.

HEDIGER, HEINI

1928. Die Tierwelt auf einer marokkanischen Farm. Blätt. Aquar.-Terrar.-Kunde, **39**, pp. 406-408.

1935. Herpetologische Beobachtungen in Marokko. Verhandl. Naturf. Ges. Basel, **46**, pp. 1-49, figs. 1-2, photo.

1937. Herpetologische Beobachtungen in Marokko. II. Zur Herpetofauna der Umgebung von Ouezzan (und Tanger). Verhandl. Naturf. Ges. Basel, **48**, pp. 183-192.

HELDT, H.

1933. La Tortue Luth *Sphargis coriacea* (L). Captures faites sur les Côtes tunisiennes (1930-1933). Contribution à l'Étude anatomique et biologique de l'Espèce. Ann. Stat. Océanogr. Salammbo (Tunis), **8**, pp. 1-40, figs. 1-17.

HELLMICH, WALTER

1955. Auf herpetologischer Forschungsfahrt in Angola (Portugiesisch-Westafrika). Aquar.-Terrar.-Zeitsch. (Datz) reprinted from 1954-1955, pp. 1-16.

HESSE, PAUL

1889. Ueber einige Reptilien des unteren Congogebiets. Zool. Garten, **30**, pp. 257-267.

HEWITT, JOHN

1914a. Notes on the Distribution and Characters of Reptiles and Amphibians in South Africa, considered in Relation to the Problem of Discontinuity Between Closely Allied Species. S. Afr. Jour. Sci., **10**, pp. 238-253, maps.

1931. Descriptions of some African Tortoises. Ann. Natal Mus., **6**, pp. 461-506, figs. 1-5, pls. xxxvi-xxxviii.

1933b. On the Cape Species and Subspecies of the Genus *Chersinella* Gray. Part I. Ann. Natal Mus., **7**, pp. 255-293, figs. 1-12, pls. xiv-xv.

1934. On the Cape Species and Subspecies of the Genus *Chersinella* Gray. Part II. Ann. Natal Mus., **7**, pp. 303-349, pls. xvi-xvii.

1935. Some new Forms of Batrachians and Reptiles from South Africa. Rec. Albany Mus., **4**, pp. 283-357, pls. xxvii-xxxvi.

1937a. A Note on the Relationship of the Cape Genera of Land-Tortoises. S. Afr. Jour. Sci., **33**, pp. 788-796, figs. 1-5, pl. x.

1937e. A Guide to the Vertebrate Fauna of the Eastern Cape Province, South Africa. Part II. Reptiles, Amphibians and Freshwater Fishes. Grahamstown, pp. 1-118, App. pp. A-B, G-H, pls. i-xxviii (Fishes, pp. 119-141, pls. xxix-xxxiv are by another author).

HULL, R. L.

1942. The Names of some Birds and Reptiles in Several Nyanza Languages. Jour. E. Afr. Uganda Nat. Hist. Soc., **16**, p. 125.

HUMMEL, K.

1929. Die fossilen Weichschildkröten (Trionychia). Eine morphologisch-systematische und stammesgeschichtliche Studie. Geol. Palaeont. Abhandl. (N.S.), **16**, pp. 359-487. (1-131 in sep.)

INGRAMS, W. H.

1931. Zanzibar, its History and People. London, pp. 1-527, figs., 12 pls.

IRVINE, F. R.

1947. The Fishes and Fisheries of the Gold Coast. London, xvi + 352 pp., figs. 1-217, map.

JAN, GEORG

1857. Cenni sul Museo Civico di Milano ed Indice sistematico dei Rettili ed Anfibi esposti nel medesimo. Milano, pp. 1-61, chart.

JEUDE, T. W. VAN LIDTH DE

1893. On a new Species of the Genus *Testudo*. Notes Leyden Mus., **15**, pp. 312-314, pl. ix.

1898. Catalogue osteologique des Poissons, Reptiles et Amphibies. Mus. Hist. Nat. Pays-Bas, **10**, Pt. II, pp. 1-54 + 1-52 + 1-11. (Pagination is repeated for each group.)

JOHNSON, W. D. and S. C.

1907. Reptile Life. Gowans & Gray, Glasgow, pp. 1-77 (excellent photographs with a minimum of letterpress).

JOHNSTON, H. H.

1897, British. Central Africa. London, xx + 544 pp., 220 illus., 6
1898. maps. (The 1898 edition is substantially the same as the 1897 so far as herpetology is concerned, but pagination differs.)

1906. Liberia. London, **1**, pp. 1-520; **2**, pp. 521-1183, 454 illus., 22 maps.

1908. George Grenfell and the Congo. London, **1**, xxiii + 496 pp.; **2**, pp. i-xx + 497-900, 496 illus., 14 maps.

KAMMERER, PAUL

1906. Eine Naturforscherfahrt durch Aegypten und den Sudan. Wochenschr. Aquar.-Terrar.-Kunde, Braunschweig, **3**, pp. 48-51, etc.

1908a. Ueber gefangene Landschildkröten. Blätt. Aquar.-Terrar.-Kunde, **19**, pp. 737-742, figs. 1-5, photos.

1908b. Schildkrötenzucht. Blätt. Aquar.-Terrar.-Kunde, **19**, pp. 757-763, figs. 1-4.

1908c. Ueber gefangene Landschildkröten. Blätt. Aquar-Terrar.-Kunde, **19**, pp. 769-778, figs. 6-15.

KANBERG, HANS

1936. Ueber einige zum Teil seltene Schildkröten aus Indien, China und Ost-Africa. Aquarium (Berlin), **10**, pp. 185-189, photos. 6025-6028.

KEHL, RAYMOND

1935a. Étude préliminaire du Cycle sexuel de quelques Reptiles sahariens. Bull. Soc. Hist. Nat. Afr. Nord (Alger), (3), **26.** pp. 61-67.

KERCADO, COMTE DE

1875. Sept oeufs de Tortue mauresque. Actes Soc. Linn. Boudeaux, **30.** p. xxxv.

KERVILLE, H. GADEAU DE

1908. Voyage zoologique en Khroumire (Tunisie) . . . 1906. Paris, xviii + 316 pp., illus., map.

KNORR, G. W.

1766-1767. Deliciae naturae selectae. Nürnberg, **1** and **2.** xx + 143 pp., pls. i-lxi (N.B. vol. **2** deals with invertebrates, etc. A second edition was printed in 1778).

KOENIG, AUGUST

1892. Die Kriechthierfauna Tunesiens. Sitzungsb. Niederrhein. Ges. Naturf. Bonn *in* Verh. Naturhist. Verein (Bonn), **49.** pp. 3-26.

1895. Reisen und Forschungen in Algerien. Bernburg, pp. 1-426, pls., map.

KOLLMAN, MAX

1912. Anomalie des Voies biliares chez une Tortue (*Clemnys* [*sic*] *leprosa*). Bull. Soc. Zool. France, **37.** pp. 101-106, figs. 1-4.

KUHL, HEINRICH

1820. Beiträge zur Zoologie und vergleichenden Anatomie . . . Frankfurt a. M., pp. 1-151 + 1-213, pls. i-xi. (Two vols. in one, Abt. II is by both Kuhl and van Hasselt.)

LABOUYSSE, ALAIN

1857. Lettre sur les Moeurs et les Habitudes des Tortues d'eau douce et des Tortues terrestres de l'Algérie. Ann. Sci. Phys. Nat. Agric. Indust. (Soc. Imp. Agric.) Lyon (3), **1.** pp. 83-98.

LACÉPÈDE, B. G. E. DE

1788. Histoire naturelle des Quadrupèdes ovipares et des Serpens. Paris, **1.** pp. 1-651, pls. i-xli, table: Synopsis methodica opp. p. 619.

LALLEMANT, CHARLES

1867. Erpétologie de l'Algérie ou Catalogue synoptique et analytique des Reptiles et Amphibiens de la Colonie. Paris. Not seen; this rare work was published by F. Sary, rue Haute-Feville 21, Paris.

LAMPE, EDUARD

1901. Catalog der Reptilien-Sammlung (Schildkröten, Crocodile, Eidechsen und Chamaeleons) des Naturhistorischen Museums zu Wiesbaden. Jahrb. Nassau. Ver. Naturk. (Wiesbaden), **54.** pp. 177-218, pl. iii.

1911. Erster Nachtrag zum Katalog der Reptilien- und Amphibien Sammlung des Naturhistorischen Museums der Stadt Wiesbaden. Jahrb. Nassau. Ver. Naturk. (Wiesbaden), **64**, pp. 137-236.

LATASTE, FERNAND

1886. Description d'une Tortue nouvelle du Haut Sénégal (*Homopus Nogueyi*). Le Naturaliste, (2), **8**, pp. 286-287.

1888a. Description d'une Tortue nouvelle originaire du Haut-Sénégal (*Cinixys Dorri*, n. sp.). Le Naturaliste (2), **10**, pp. 164-166, figs. 1-3.

LATROBE, C. I.

1818. Journal of a Visit to South Africa in 1815 and 1816, etc. London, vii + 406 pp., pls. i-xvi, map (reprinted 1821).

LAURENT, PAUL

1935. Contribution à la Connaissance de la Faune des Vertébrés du Maroc (Batraciens, Reptiles, Mammifères). Bull. Soc. Hist Nat. Afr. Nord (Alger), **26**, pp. 344-359.

LAURENT, RAYMOND

1950f. Reptiles et Batraciens de la Région de Dundo (Angola du Nord-Est). Première Note. Museu do Dundo. Publ. Culturais da Companhia de Diamantes de Angola, No. 6, pp. 127-136.

1953a. Reptiles et Batraciens récemment parvenus au Musée royal du Congo belge. Bull. Cercle Zool. Congo., **21**, pp. 21-29.

1954d. Aperçu de la Biogéographie des Batraciens et des Reptiles de la Région des Grands Lacs. Bull. Soc. Zool. France, **79**, pp. 290-310.

LEAKEY, B. E.

1944. Some Notes on the Breeding Habits of the Leopard Tortoise (*Testudo pardalis* Bell). Jour. E. Afr. Uganda Nat. Hist. Soc., **17**, pp. 396-398, figs.

LEBLANC, E.

1919. Note sur les Plexus choroïdes chez les Reptiles. Bull. Soc. Hist. Nat. Afr. Nord (Alger), **10**, pp. 177-184, figs. 1-6.

LICHTENSTEIN, M. H. C.

1823. Verzeichniss der Dubletten des Zoologischen Museums der . . . Universität . . . Berlin, x + 118 pp., pl.

LICHTENSTEIN, M. H. C. and EDUARD VON MARTENS

1856. Nomenclator Reptilium et Amphibiorum Musei zoologici berolinensis. Berlin, i-iv + 1-48 pp.

LINDHOLM, W. A.

1906. Beschreibung einer neuen Schildkrötenart aus Deutsch-Südwestafrika nebst Bemerkungen über die Gattung *Homopus* D. et B. Jahrb. Nassau. Ver. Naturk. (Wiesbaden), **59**, pp. 345-351.

1929. Revidiertes Verzeichnis der Gattungen der rezenten Schildkröten nebst Notizen zur Nomenklatur einiger Arten. Zool. Anz., **81**, pp. 275-295.

LINNAEUS, CARL VON

1758. Systema Naturae. Holmiae, ed. 10, **1**, pp. 1-824.

1766. Systema Naturae. Halae Magdeburgicae, ed. 12, **1**, pp. 1-532.

LÖNNBERG, EINAR

1896. Linnean Type-Specimens of Birds, Reptiles, Batrachians and Fishes in the Zoological Museum of the R. University of Upsala. Bihang Kongl. Svenska Vetensk.-Akad. Handl. (Stockholm), **22**, Pt. iv, No. 1, pp. 1-45.

1907. Reptilia and Batrachia. *In* Sjöstedt, Y., Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaisteppen 1905-1906. Upsala, No. 4, pp. 1-28, pl. i.

1911. Reptiles, Batrachians and Fishes collected by the Swedish Zoological Expedition to British East Africa 1911. K. Svenska Vetensk.-Akad. Handl. (Stockholm), **47**, No. 6, pp. 1-42, pls. i-ii. (Batrachians by Andersson, L. G.)

LORTET, LOUIS

1887. Observations sur les Tortues terrestres et paludines du Bassin de la Méditerranée. Arch. Mus. Hist. Nat. Lyon, **4**, pp. 1-26, pls. i-vii.

LOVERIDGE, ARTUHR

1921d. Notes on Tortoises collected in East Africa 1915-1919. Jour. E. Afr. Uganda Nat. Hist. Soc., No. 16, pp. 50-52.

1922d. Notes, on pp. 522-524 of J. B. Procter, 1922b, which see.

1923g. Notes on East African Tortoises Collected 1921-1923, with the Description of a New Species of Soft Land Tortoise. Proc. Zool. Soc. London, pp. 923-933, pls. i-ii.

1924b. Check List of the Reptilia Recorded from the British Territories in East Africa. Jour. E. Afr. Uganda Nat. Hist. Soc., Spec. Suppl. No. 3, pp. 1-16.

1928d. Field Notes on Vertebrates Collected by the Smithsonian-Chrysler East African Expedition. Proc. U. S. Nat. Mus., **73**, Art. 17, pp. 1-69, pls. i-iv.

1929h. East African Reptiles and Amphibians in the United States National Museum. Bull. U. S. Nat. Mus., No. 151, pp. 1-135, pl. i.

1933h. Reports on the Scientific Results of an Expedition to the Southwestern Highlands of Tanganyika Territory. VII. Herpetology. (This part of vol. **74** appeared *after* **75**!). Bull. Mus. Comp. Zool., **74**, pp. 197-416, pls. i-iii.

1935c. Scientific Results of an Expedition to Rain Forest Regions in Eastern Africa. I. New Reptiles and Amphibians from East Africa. Bull. Mus. Comp. Zool., **79**, pp. 1-19.

1936h. African Reptiles and Amphibians in the Field Museum of Natural History. Field Mus. Nat. Hist., Zool. Ser., **22**, pp. 1-111.

1936j. Scientific Results of an Expedition to Rain Forest Regions in Eastern Africa. V. Reptiles. Bull. Mus. Comp. Zool., **79**, pp. 209-337, pls. i-ix.

1937c. Zoological Results of the George Vanderbilt African Expedition of 1934. Part VII. Reptiles and Amphibians. Proc. Acad. Nat. Sci. Philadelphia, **89**, pp. 265-296.

1937f. Scientific Results of an Expedition to Rain Forest Regions in Eastern Africa. IX. Zoogeography and Itinerary. Bull. Mus. Comp. Zool., **79**, pp. 481-541, pls. i-iv.

1941e. Report on the Smithsonian-Firestone Expedition's Collection of Reptiles and Amphibians from Liberia. Proc. U. S. Nat. Mus., **91**, pp. 113-140.

1942e. Scientific Results of a Fourth Expedition to Forested Areas in East and Central Africa. IV. Reptiles. Bull. Mus. Comp. Zool., **91**, pp. 237-273, pls. i-vi.

1947g. Bone-making Material for Turtles. Copeia, p. 136.

1949b. Some Queer Adaptations of African Animals. Nyasaland Jour., **2**, No. 2, pp. 9-22.

1952a. Mission A. Villiers au Togo et du Dahomey (1950). XII. Tortoises and Lizards. Bull. Inst. franc. Afrique noire, **14**, pp. 229-242.

1953e. Zoological Results of a Fifth Expedition to East Africa. III. Reptiles from Nyasaland and Tete. Bull. Mus. Comp. Zool., **110**, pp. 141-322, pls. i-v.

MASI, LUIGI

1911a. Notizie su alcuni Cheloni donati al R. Museo Zoologico di Roma. Boll. Soc. Zool. Italiana Roma, (2), **12**, pp. 29-39.

MATSCHIE, PAUL

1893c. Die Reptilien und Amphibien des Togogebietes. Mitt. Fors. Gel. deutschen Schutzgeb., **6**, pp. 207-215.

MAYET, VALERY

1903. Catalogue raisonnée des Reptiles et Batraciens de la Tunisie. *In* Exploration Scientifique de la Tunisie. Paris, pp. 1-32.

MEEK, S. E.

1897. List of Fishes and Reptiles obtained by Field Columbian Museum East African Expedition to Somali-land in 1896. Field Columbian Mus., Zool. Ser., **1**, pp. 161-184, fig.

1910. Batrachians and Reptiles from British East Africa. Field Mus. Nat. Hist., Zool. Ser., **7**, pp. 403-414.

MELLIS, J. C.

1875. St. Helena: A Physical, Historical, and Topographical Description of the Island. London, xiv + 426 pp., illus.

MERREM, BLASIUS

'1820. Versuch eines Systems der Amphibien. Tentamen Systematis Amphibiorum. Marburg, xvi + 191 pp., pl. i.

MERTENS, ROBERT

1922a. Verzeichnis der Typen in der herpetologischen Sammlung des Senckenbergischen Museums. Senckenbergiana, **4**, pp. 162-183.

1924b. Ueber die Reptilien- und Amphibien-Sammlung des Zoologischen Gartens in London. Pallasia, **2**, pp. 67-72.

1926a. Herpetologische Mitteilungen VIII-XV. XIV. Zur Kenntnis der Herpetofauna von Angola. Senckenbergiana, **8**, pp. 137-155.

1936b. Eine bemerkenswerte Variation des Schildkrötenpanzers. Isis, pp. 15-18, figs. 1-3.

1937b. Reptilien und Amphibien aus dem südlichen Inner-Afrika. Abhandl. Senckenberg. Naturf. Ges., No. 435, pp. 1-23.

1937d. Über eine herpetologische Sammlung aus dem Gebiete des Njarasa-Grabens Ost-Afrika. Veröffentl. deutschen Kolon.-Übersee-Mus. Bremen, **2**, pp. 1-9.

1938b. Herpetologische Ergebnisse einer Reise nach Kamerun. Abhandl. Senckenberg. Naturf. Ges., No. 442, pp. 1-52, pls. i-x.

1938e. Amphibien und Reptilien aus Angola. Senckenbergiana, **20**, pp. 425-442, figs. 1-6.

1940c. Der Knochenpanzer einer kyphotischen Weichschildkröte. Senckenbergiana, **22**, pp. 236-243, figs. 1-5.

1942d. Über das Verhalten der Spaltenschildkröte *Malacochersus tornieri* (Siebenrock). Zool. Garten (Leipzig), (N.F.), **14**, pp. 245-251, figs. 1-4.

1946b. Die Warn- und Droh-Reaktionen der Reptilien. Abhandl. Senckenberg. Naturf. Ges., No. 471, pp. 1-38, pls. i-viii.

1946d. Über einige mediterrane Schildkröten-Rassen. Senckenbergiana, **27**, pp. 111-118, figs. 1-3.

1955a. Die Amphibien und Reptilien Südwestafrikas. Aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. Abhandl. Senckenberg. Naturf. Ges., No. 490, pp. 1-172, pls. i-xxiv, map.

1955b. Amphibien und Reptilien aus Ostafrika. Jahresber. Vereins vaterl. Naturk. Württemberg, **110**, pp. 47-61.

MERTENS, ROBERT and LORENZ MÜLLER *in* H. T. RUST

1934a. Systematische Liste der lebenden Schildkröten. Blätt. Aquar.-Terrar.-Kunde, **45**, pp. 42-45, 59-67 (repaged 1-12 in reprint, which pagination is the one cited in text).

MERTENS, ROBERT and HEINZ WERMUTH

1955. Die rezenten Schildkröten, Krokodile und Brückenechsen. Zool.

Jahrb. Syst., **83**, pp. 323-440. (Though published 31.x.55, this checklist was not received at Harvard until 3.i.56, too late for citation under genera and species.)

MITCHELL, B. L.

1946. A Naturalist in Nyasaland. Nyasaland Agric. Quart. Jour., **6**, pp. 1-47.

MOCQUARD, FRANCOIS

1897b. Sur une Collection de Reptiles recueillie par M. Haugh à Lambaréné. Bull. Soc. Philom. Paris, (8), **9**, pp. 5-20.

1899a. Reptiles rapportés de l'Afrique australe et centrale par M. Édouard Foá. Bull. Mus. Hist. Nat. (Paris), **5**, pp. 218-219.

1906a. (1905) La Faune herpétologique du Congo français. Revue Coloniale (Ministere des Colonies, Paris), pp. 477-485, 554-564, 603-614, 668-674 (reprinted as pp. 1-39).

1908b. Reptiles du Zambèze et des Grandes Lacs. *In* É. Foá, Résultats scientifiques des Voyages en Afrique d'Édouard Foá. Paris, pp. 557-558, map.

MOHRING, C. A.

1824. Descriptio Trionychos aegyptiaca osteologica. Berlin. (A latin dissertation: not seen.)

MONARD, ALBERT

1931. Mission scientifique Suisse dans l'Angola. Résultats scientifiques. Reptiles. Bull. Soc. Neuchâtel. Sci. Nat., **55**, pp. 89-111, figs. 1-5.

1937b. Contribution à l'Herpétologie d'Angola. Arqu. Museu Bocage (Lisboa), **8**, pp. 1-154, figs. 1-3.

1951. Résultats de la Mission Zoologique Suisse au Cameroun. Mem. Inst. Franç. Afrique Noire, **1**, pp. 123-185.

MOREAU, R. E. and R. H. W. PAKENHAM

1941. (1940) The Land Vertebrates of Pemba, Zanzibar, and Mafia: a Zoogeographical Study. Proc. Zool. Soc. London, **100 (A)**, pp. 97-128, fig. 1.

MOSAUER, WALTER

1934. The Reptiles and Amphibians of Tunisia. Publ. Univ. Calif. Biol. Sci., **1**, pp. 49-64, fig., map.

MOURGUE, MARCEL

1920. Reptiles recueillis de Mai à Juin au cours d'une Excursion zoologique en Tunisie. Bull. Soc. Zool. France, **45**, pp. 233-235.

MOYLE, VIVIEN

1949. Nitrogenous Excretion in Chelonian Reptiles. Biochem. Jour., Cambridge, **44**, pp. 581-584.

MÜLLER, FRIEDRICH

1882a. Erster Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. Verhandl. Naturf. Ges. Basel, **7**, pp. 120-165, pls. ix-xi.

1887a. Fünfter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. Verhandl. Naturf. Ges. Basel, **8**, pp. 249-296, pls. i-iii.

1890. Sechster Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. Verhandl. Naturf. Ges. Basel, **8**, pp. 685-705, pl. x.

1892. Siebenter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. Verhandl. Naturf. Ges. Basel, **10**, pp. 195-215, pls. iii-iv.

MÜLLER, LORENZ

1910. Beiträge zur Herpetologie Kameruns. Abhandl. K. Bayer. Akad. Wiss., Kl. 2, **24**, pp. 543-626, pl.

1939a. Über Variation und Systematik einiger südafrikanischer Landschildkröten der *Geometrica*-Gruppe. Abhandl. Ber. Mus. Naturk. Vorgesch. Naturwiss. Ver. Magdeburg, **7**, pp. 129-164, pls. x-xi.

MÜLLER, P. L. S.

1774. Vollständiges Natursystem. Nürnberg, **3**, 350 + [16] pp.

NEUMANN, OSCAR

1905. Über nordost-afrikanische und arabische Kriechtiere. Zool. Jahrb., Abt. Syst., **22**, pp. 389-404.

NIEDEN, FRITZ

1913c. Neues Verzeichnis der Kriechtiere (ausser den Schlangen) von Deutsch-Ostafrika. I. Reptilia. Mitt. Zool. Mus. Berlin, **7**, pp. 51-100.

NOËL-HUME, IVOR and AUDREY

1954. Tortoises, Terrapins and Turtles. Foyles Handbooks. London, pp. 1-112, figs. 1-19.

ODHNER, TEODOR

1908. Reptilien und Batrachier, gesammelt von Dr. I. Trägardh in Natal und Zululand 1904-05. Arkiv Zool., **4**, No. 18, pp. 1-7.

OLIVIER, ERNEST

1894. Herpétologie algérienne ou Catalogue raisonné des Reptiles et des Batraciens observés jusqu'à ce Jour en Algérie. Mém. Soc. Zool. France, **7**, pp. 89-131.

1896b. Matériaux pour la Faune de la Tunisie. I. Catalogue de Reptiles. Revue Sci. Bourbonnais France (Moulins), **9**, pp. 117-128.

OUDEMANS, J. T.

1895. Einige Bemerkungen über zwei südafrikanische Schildkröten. Zool. Anz., **18**, pp. 321-324.

PARENTI, PAOLO and LUIGI PICAGLIA

1886. Rettili ed Anfibi raccolti de P. Parenti nel Viaggio di Circumnavigaione della R. Corvetta "Vettor Pisani", Comandante G. Palumbo, negli Anni 1882-85 e da V. Ragazzi sulle Coste del

Mar Rosso e dell' America meridionale negli Anni 1879-84. Atti Soc. Nat. Modena (3), **5**, pp. 26-96.

PARKER, H. W.

1932a. Scientific Results of the Cambridge Expedition to the East African Lakes, 1930-1931. 5. Reptiles and Amphibians. Jour. Linn. Soc. London, Zool., **38**, pp. 213-229, figs. 1-10.

1932b. Two Collections of Reptiles and Amphibians from British Somaliland. Proc. Zool. Soc. London, pp. 335-367, figs. 1-3.

1939. Turtles Stranded on the British Coast 1938-1939. Proc. Linn. Soc. London, Session 151, pp. 127-129.

PARKER, H. W., R. E. MOREAU and R. H. W. PAKENHAM

1940. Notes on the Herpetology of the East African Islands. Ann. Mag. Nat. Hist., (11), **5**, pp. 309-314.

PECHUËL-LOESCHE, EDUARD

1882. Die Loango-Expedition. Leipzig, Part III, pp. 1-503, figs., pls., maps. (Parts I and II appeared in 1879.)

PEEL, C. V. A.

1900. Somaliland. London, xv + 345 pp., figs., pl., map.

PELLEGRIN, JACQUES

1909b. Reptiles du Soudan récoltés par la Mission Tilho-Gaillard. Description d'une Espèce nouvelle. Bull. Mus. Hist. Nat. (Paris), **15**, pp. 413-415, fig. 1.

1912a. Reptiles, Batraciens et Poissons du Maroc (Mission de Mme Camille du Gast). Bull. Soc. Zool. France, **37**, pp. 255-262.

1912b. Reptiles, Batraciens et Poissons du Maroc (Récoltés par le Dr. H. Millet). Bull. Soc. Zool. France, **37**, pp. 262-264.

1913. (1912) Les Vertébrés des Eaux douces du Maroc. Comptes Rendus Assoc. Franc. Avanc. Sci. Nîmes, **41**, pp. 419-424.

1914. (1913) Les Vertébrés des Eaux douces du Sahara. Comptes Rendus Assoc. Franc. Avanc. Sci. Tunis, **42**, pp. 346-352.

1914. Reptiles et Batraciens recueillis par la Mission Tilho (Niger-Tchad). *In* Documents scientifiques de la Mission Tilho 1906-1909, **3**, pp. 121-129, fig., pl. i (reptiles).

1926a. (1925) Liste des Reptiles, Batraciens et Poissons d'Eau douce des Collections du Musée de l'Institut scientifique chérifien à Rabat. Bull. Soc. Sci. Nat. Maroc (Rabat), **5**, pp. 315-321.

1926c. La Longévité chez les Reptiles en Captivité. Revue Gen. Sci. (Paris), **37**, pp. 47-49.

1926e. Mission J. Pellegrin au Maroc. Reptiles, Batraciens et Poissons. Bull. Mus. Hist. Nat. (Paris), **32**, pp. 120-124.

1927a. Les Reptiles et les Batraciens de l'Afrique du Nord française. Comptes Rendus Assoc. Franc. Avanc. Sci. Constantine, **51**, pp. 260-264.

PETERS, W. K. H.

1854a. Übersicht der auf seiner Reise nach Mossambique beobachteten Schildkröten. Monatsber. Akad. Wiss. Berlin, pp. 215-216.

1862b. Über die von dem so früh in Afrika verstorbenen Freiherrn von Barnim und Dr. Hartmann auf ihrer Reise durch Aegypten, Nubien und dem Sennar gesammelten Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 271-279, pl.

1866b. Übersicht der aus dem Nachlass des Baron Carl von der Decken stammenden und auf seiner ostafrikanischen Reise gesammelten Säugethiere und Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 884-892.

1869a. Amphibien. *In* Decken, C. C., Reisen in Ost-Afrika. Leipzig, **3**, Abt. **1**, pp. 11-18, pls. i-ii (A reprint of 1866b plus pls.).

1873e. Über eine von Hrn. F. Pollen und van Dam auf Madagascar und anderen ostafrikanischen Inseln gemachte Sammlung von Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 792-795.

1875a. Über die von Hrn. Professor Dr. R. Buchholz in Westafrika gesammelten Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 196-212, pls, i-iii.

1876a. Eine zweite Mittheilung über die von Hrn. Professor Dr. R. Buchholz in Westafrika gesammelten Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 117-123, pl. i.

1877e. Übersicht der Amphibien aus Chinchoxo (Westafrika) welche von der afrikanischen Gesellschaft dem berliner zoologischen Museum übergeben sind. Monatsber. Akad. Wiss. Berlin, pp. 611-621, pl.

1878a. Über die von Hrn. J. M. Hildebrandt während seiner letzten ost-afrikanischen Reise gesammelten Säugethiere und Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 194-209, pls. i-ii.

1880d. Über die von Hrn. Gerhard Rohlfs und Dr. A. Stecker auf der Reise nach der Oase Kufra gesammelten Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 305-309.

1881a. Amphibien der Expedition nach Kufra. *In* Rohlfs, G., Kufra. Leipzig, pp. 1-559, charts 1-21, maps. (Reprint of 1880d).

1882a. Naturwissenschaftliche Reise nach Mossambique auf Befehl seiner Majestät des Königs Friedrich Wilhelm IV in den Jahren 1842 bis 1848 ausgeführt. Zoologie, **3**, Amphibien. Berlin, xv + 191 pp., pls. i-xxx.

PITMAN, C. R. S.

1934. A Check List of Reptilia and Amphibia Occurring and Believed to Occur in Northern Rhodesia. *In* Pitman, C. R. S., Report on a Faunal Survey of Northern Rhodesia. Livingstone, xii + 500 pp. + Index of i-xxxii, maps A-K.

1942b. A Game Warden takes Stock. London, xvii + 287 pp. pls.

Poiret, J. L. M.

1789. Voyage en Barbarie ou Lettres écrites de l'Ancienne Numidie. **2**, pp. 1-363. (Appendix on "amphibiens" on pp. 283-290.)

Power, J. H.

1927c. On the Herpetological Fauna of the Lobatsi-Linokana Area. Part I. Trans. Roy. Soc. S. Africa, **14**, pp. 405-422, fig. 1, pls. xviii-xxii, map.

1931. Part II, *Ibid*, **20**, pp. 39-49, figs. 1-2.

1932b. *Testudo verreauxii* Smith; a Study in Variation. S. Afr. Jour. Sci., **29**, pp. 466-472.

1933a. Herpetological Notes and Records. I. Trans. Roy. Sci. S. Africa, **21**, pp. 211-220, map.

Prato, Alberto del

1895. Vertebrati Eritri aggiunta al Catalogo della Collezione Eritrea Bottego. Atti Soc. Ital. Sci. Nat. (Milano), **35**, pp. 17-26, figs. 1-2.

Procter, J. B.

1922b. A Study of the remarkable Tortoise, *Testudo loveridgii* Blgr., and the Morphology of the Chelonian Carapace. Proc. Zool. Soc. London, pp. 483-526, figs. 1-21, pls. i-iii.

Rawitz, Bernhard

1915. Das zentrale Nervensystem einiger madagassischer Reptilien. *In* Voeltzkow, A., Reise in Ostafrika in den Jahren 1903-1905. Stuttgart, **4**, pp. 279-332, pls. xx-xxiii.

Reichenow, Anton

1874. Eine Sammlung Lurche und Kriechthiere von Westafrika. Arch. Naturg., **40**, Abt. 1, pp. 287-298, pl. ix.

1878. Über einige nachträglich von der deutschen Expedition nach der Loango-Küste eingegangene Reptilien und Fische. Sitzungsb. Naturf. Freunde Berlin, p. 92.

Rochebrune, A. T. de

1884a. Faune de la Sénégambie. Reptiles. Paris, pp. 1-221, pls. i-xx. (The most unreliable work on African herpetology.)

Rose, Walter

1929. Veld and Vlei. Cape Town, xxiii + 240 pp., figs., photos 1-125.

1950. The Reptiles and Amphibians of Southern Africa. Cape Town, xxviii + 378 pp., frontis. and photos 1-213.

Roux, Jean

1910. Reise von Dr. J. Carl im nördlichen zentral-afrikanischen Seengebiet. Reptilien und Amphibien. Revue Suisse Zool. (Genève), **18**, pp. 95-103.

Rozet, C. A.

1833. Voyage dans la Régence d'Alger . . . l'Histoire naturelle, etc. Paris, **1**, pp. 1-286, pls. i-xxx.

RUCKES, HERBERT

1937. The Lateral Arcades of Certain Emydids and Testudinids. Herpetologica (San Diego), **1**, pp. 97-103, pl. x.

RÜPPELL, EDWARD (W. P. E. S.)

1835. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. III. Amphibien. Frankfurt a. M., pp. 1-18, pls. i-vi.

1845a. Beschreibung und Abbildung einer neuen Art von Landschildkröten, zur Gattung *Kinixys* gehörig. Mus. Senckenberg., **3**, pp. 223-292, pl. xvi.

1845b. Verzeichniss der in dem Museum der Senckenbergischen Gesellschaft aufgestellten Sammlung. Amphibien. Mus. Senckenberg., **3**, pp. 293-316.

RUST, H. T.

1937. Interessante Schildkröten. IV. Die Gattung *Homopus* Duméril et Bibron, 1834. Wochenschr. Aquar.-Terrar.-Kunde (Braunschweig), **34**, pp. 699-700, photos.

SAUVAGE, H. E.

1884b. Notice sur une Collection de Reptiles et de Poissons recueillie à Mayumba, Congo. Bull. Soc. Zool. France, **9**, pp. 199-208, pl. vi.

SCHEPERS, G. W. H.

1938. The External Morphology of the Brain of *Testudo geometrica*. Jour. Anat. (Cambridge, Eng.), **72**, pp. 535-555, figs. 1-5.

1939. The Blood Vascular System of the Brain of *Testudo geometrica*. Jour. Anat. (Cambridge, Eng.), **73**, pp. 451-495, figs. 1-8.

1948a. A Dorso-lateral Invagination of the Olfactory Bulb in *Testudo geometrica*. S. Afr. Jour. Sci. (Johannesburg), **2**, pp. 9-11, figs. 1-4.

1948b. Evolution of the Forebrain. The Fundamental Anatomy of the Telencephalon, with Special Reference to that of *Testudo geometrica*. Cape Town, pp. 1-212, figs. 1-250.

SCHERER, JOSEPH

1902. Herpetologische Reiseskizzen aus Zentral-Ost-Afrika. Blätt. Aquar.-Terrar.-Kunde, **13**, pp. 238-242, 253-255, 263-267, figs.

SCHLEGEL, HERMANN

1841. Bemerkungen über die in der Regentschaft Algier gesammelten Amphibien. Pp. 106-139, *in* Wagner, Moritz, Reisen in der Regentschaft Algier in den Jahren 1836, 1837 und 1838. Leipzig, **3**, pp. 1-296.

SCHMIDT, K. P.

1919. Contributions to the Herpetology of the Belgian Congo Based on the Collection of the American Museum Congo Expedition 1909-1915. Part I. Turtles, Crocodiles, Lizards and Chameleons. Bull. Amer. Mus. Nat. Hist., **39**, pp. 385-624, figs. 1-27, pls. vii-xxxii.

1933. The Reptiles of the Pulitzer Angola Expedition. Ann. Carnegie Mus., **22**, pp. 1-15, figs. 1-2, pls. i-ii.

SCHNEIDER, J. G.

1792. Beschreibung und Abbildung einer neuen Art von Wasserschildkröte nebst Bestimmungen einiger bisher wenig bekannten fremden Arten. Ges. Naturf. Freunde Berlin, **10**, pp. 259-284, pl. vii.

SCHOEPFF, J. D.

1792. Naturgeschichte der Schildkröten mit Abbildungen erläutert. Erlangae, 12 + 160 pp., pls. i-xxxii (? xxxiii-xxxiv).

1792-1801. Historia Testudinum. Erlangae, xii + 136 pp., pls. i-xxxii (? xxxiii-xxxiv).

SCHWEIGGER, A. F.

1812. Monographiae Cheloniorum. Königsberger Arch. Naturwiss. Math., **1**, pp. 271-368, 406-458.

1814. Prodromi Monographiae Cheloniorum. Regiomonti, vi + 58 pp. (partial reprint of 1812).

SCLATER, P. L.

1871b. On Additions to the Menagerie. Proc. Zool. Soc. London, pp. 543-546.

1872. On Additions to the Society's Menagerie. Proc. Zool. Soc. London, pp. 602-609.

SCLATER, W. L.

1898. List of the Reptiles and Batrachians of South Africa, with Descriptions of New Species. Ann. S. African Mus., **1**, pp. 95-108, pl. v.

SCORTECCI, GIUSEPPE

1928b. Rettili dell'Eritrea esistenti nelle Collezioni del Museo Civico di Milano. Atti. Soc. Ital. Sci. Nat. (Milano), **67**, pp. 290-339, figs. 1-8, pls. vii-ix.

1930a. Rettili ed Anfibi raccolti dal Prof. E. Zavattari in Eritrea. Atti. Soc. Ital. Sci. Nat. (Milano), **69**, pp. 193-217, figs.

1940a. Reptilia. *In* Missione biologica nel paese dei Borana raccolte zoologiche. (Reale Accad. d'Italia, Roma), **2**, pp. 125-150 (repaged 5-30 in reprint).

1943. Reptilia. *In* Missione biologica Sagan-Omo. Zoologia. Roma, pp. 267-305.

SEBA, ALBERTUS

1735. Locupletissimi Rerum Naturalium Thesauri Accurata Descriptio, et Iconibus Artificiosissimis Expressio, per Universam Physices Historiam, etc. Amstelaedami, **2**, xxx + 154 pp., pls. i-cxiv.

SEURAT, L. G.

1918. Nématodes de la Clemmyde lépreuse. Bull. Soc. Hist. Nat. Afr. Nord (Alger), **9**, pp. 20-26.

1925a. *Cistudo europaea* aux Environs de la Calle. Bull. Soc. Hist. Nat. Afr. Nord (Alger), **16**, pp. 150-151.

1927. L'Estuaire de l'Akarit (Golfe de Gabes). Bull. Soc. Hist. Nat. Afr. Nord (Alger), **18**, pp. 80-82.

1930. Exploration zoologique de l'Algérie de 1830-1930. Paris, pp. 1-708, figs., pls. i-xvi.

SHAW, GEORGE

1802. General Zoology or Systematic Natural History. **3**, Amphibia. London, viii + 614 pp., pls. i-cxl.

SHAW, G. and F. P. NODDER

1797. Naturalists Miscellany. London, **9**, letterpress to pls. cccl-cccxlviii.

SIEBENROCK, FRIEDRICH

1897. Das Kopfskelet der Schildkröten. Sitzungsb. Akad. Wiss. Wien. **106**, Abt. **1**, pp. 245-328, pls. i-vi.

1898. Über den Bau und die Entwicklung des Zungenbein-Apparates der Schildkröten. Ann. Naturhist. Hofmus. (Wien), **13**, pp. 424-437, pls. xvii-xviii.

1899. Über den Kehlkopf und die Luftröhre der Schildkröten. Sitzungsb. Akad. Wiss. Wien, **108**, Abt. **1**, pp. 563-595, pls. i-iii.

1902b. Zur Systematik der Schildkrötenfamilie Trionychidae Bell, nebst der Beschreibung einer neuen *Cyclanorbis*-Art. Sitzungsb. Akad. Wiss. Wien, **111**, Abt. **1**, pp. 807-846, figs. 2-18.

1903a. Über zwei seltene und eine neue Schildkröte des berliner Museums. Anz. Akad. Wiss. Wien, **40**, pp. 185-186 (abstract of 1903b with description of *Testudo tornieri*).

1903b. Über zwei seltene und eine neue Schildkröte des berliner Museums. Sitzungsb. Akad. Wiss. Wien, **112**, Abt. **1**, pp. 439-445, pl.

1904b. Eine neue *Testudo*-Art der *Geometrica*-Gruppe aus Süd-afrika. Rückenschale von *Testudo tornieri* Siebenr. Sitzungsb. Akad. Wiss. Wien, **113**, Abt. **1**, pp. 29-34, fig.

1904b. Eine neue *Testudo*-Art der *Geometrica*-Gruppe aus Süd-afrika. Anz. Akad. Wiss. Wien, **41**, pp. 194-195.

1904c. Die südafrikanischen *Testudo*-Arten der *Geometrica*-Gruppe s.l. Sitzungsb. Akad. Wiss. Wien, **113**, Abt. **1**, pp. 307-323, pls. i-v.

1905a. Chelonologische Notizen. Zool. Anz., **28**, pp. 406-468, figs. 1-2.

1906a. Ergebnisse einer zoologischen Forschungsreise von Dr. Franz Werner nach Ägypten und im ägyptischen Sudan. IV. Krokodile und Schildkröten. Sitzungsb. Akad. Wiss. Wien, **115**, Abt. **1**, pp. 817-839, figs. 1-3.

1906b. Schildkröten von Ostafrika und Madagaskar. *In* Voeltzkow, A., 1906-1910, Reise in Ostafrika in den Jahren 1903-1905. Stuttgart, **2**, pp. 1-40, figs. 1-14, pls. i-v.

1906c. Zur Kenntnis der mediterranean *Testudo*-Arten und über ihre Verbreitung in Europa. Zool. Anz., **30**, pp. 847-854.

1907. Über zwei Schildkröten aus Kamerun. Ann. Naturhist. Hofmus. (Wien), **22**, pp. 1-8, fig., pl. i.

1909a. Synopsis der rezenten Schildkröten mit Berücksichtigung der in historischer Zeit ausgestorbenen Arten. Zool. Jahrb., Syst. Suppl., **10**, pp. 427-618.

1909b. *Homopus bergeri* Ldh., eine *Testudo*-Art aus der *Geometrica*-Gruppe. Zool. Anz., **34**, pp. 623-625.

1910. Schildkröten aus Süd- und Südwestafrika, gesammelt von Dr. R. Pöch und J. Brunnthaler. Sitzungsb. Akad. Wiss. Wien, **119**, Abt. 1, pp. 693-720, pls. i-iv.

1912. *Testudo chilensis* Gray und *Testudo sulcata* Mill. Verh. Zool.-Bot. Ges. Wien, **62**, pp. 214-219, figs. 1-2.

1913b. Schildkröten aus Syrien und Mesopotamien. Ann. Naturhist. Hofmus. (Wien), **27**, pp. 171-225, figs. 1-28, pls. x-xii.

1916. Schildkröten aus dem nördlichen Seengebiet und von Belgisch-Kongo. Ann. Naturhist. Hofmus. (Wien), **30**, pp. 1-12, figs. 1-2, pls. i-ii.

1919. *Emydura macquarrii* Gray und der systematische Wert des Nuchalschildes bei den Schildkröten. Zool. Anz., **50**, pp. 273-276.

SJÖSTEDT, YNGVE

1897. Reptilien aus Kamerun, West-Afrika. Bihang till K. Svenska Vet.-Akad. Handl., **23**, part 4, No. 2, pp. 1-36, pls. i-iii.

SMETS, G.

1885. Notes sur trois Testudinides de l'Afrique Australe. Ann. Soc. Sci. Bruxelles, **10**, pp. 1-11.

SMITH, ANDREW

1838-1849. Illustrations of the Zoology of South Africa. Reptiles. London, pls. i-lxxviii, App., pp. 1-28.

SORDELLI, FERDINANDO

1901. Anomalia in una Testuggine (*Cinixys belliana*) del Sudan orientale. Atti Soc. Ital. Sci. Nat. (Milano), **39**, pp. 111-114, figs. 1-2.

1908. Vertebrati dell'Argentina e del Benadir donati al Civico Museo di Milano dal Sig. Silvio Bondimaj. Atti Soc. Ital. Sci. Nat. (Milano), **47**, pp. 10-22, figs.

SOWERBY, J. DE C. and EDWARD LEAR

1872. Tortoises, Terrapins, and Turtles. London, pls. i-lx (letterpress pp. 1-16 by J. E. Gray).

STAMP, L. D.

1953. Africa: A Study in Tropical Development. (New York, vii + 568 pp., figs. 1-233.

STEINDACHNER, FRANZ

1867a. Reptilien. *In* Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859, unter den Befehlen des

Commodore B. von Wullerstorf-Urbair. Zoology, **1**, pp. 1-98, pls. i-iii.

1870a. Herpetologische Notizen II. 1. Reptilien gesammelt während einer Reise in Senegambien (October bis December 1868). Sitzungsb. Akad. Wiss. Wien, **62**, Abt. **1**, pp. 326-335.

1891c. Ueber die Reptilien und Batrachier der westlichen und östlichen Gruppe der canarischen Inseln. Ann. Naturhist. Hofmus. (Wien), **6**, pp. 287-306.

1901. Expedition S. M. Schiff "Pola" in das Rothe Meer. XVII. Bericht über die herpetologischen Aufsammlungen. Denkschr. Akad. Wiss. Wien, **69**, Abt. **1**, pp. 325-335, pls. i-ii.

STEMMLER-MORATH, CARL

1952. Biologische Beobachtungen an *Clemmys leprosa* in Südmarokko. Aquar.-Terrar. Zeitschr. (Stuttgart), **5**, pp. 217-218, photos 1-2.

STERNFELD, ROBERT

1910. Die Reptilien (ausser den Schlangen) und Amphibien Kameruns. *In* Die Fauna der deutschen Kolonien. Berlin, Ser. 1, part 2, iv + 74 pp., figs. 1-155, map.

1911b. Zur Herpetologie Südwestafrikas. Mitt. Zool. Mus. Berlin, **5**, pp. 393-411.

1911d. Die Reptilien (ausser den Schlangen) und Amphibien von Deutsch-Südwestafrika. *In* Die Fauna der deutschen Kolonien. Berlin, Ser. 4, part 2, iv + 65 pp., figs. 1-76, map.

1912c. (1913) Reptilia. *In* Wiss. Ergeb. der deutschen Zentral-Afrika-Expedition 1907-1908. Leipzig (1913, but separate in 1912), **4**, pp. 197-279, figs. 1-4, pls. vi-ix.

1917. Reptilia und Amphibia. *In* Wiss. Ergeb. der zweiten deutschen Zentral-Afrika-Expedition 1910-1911. Leipzig, **1**, pp. 407-510, pls. xxii-xxiv.

STEVENSON-HAMILTON, J.

1947. Wild Life in South Africa. London, vii + 364 pp.

STRAUCH, ALEXANDRE

1862a. Chelonologische Studien, mit besonderer Beziehung auf die Schildkrötensammlung der kaiserlichen Akademie der Wissenschaften zu St. Petersburg. Mém. Acad. Imp. Sci. St.-Pétersbourg, (7), **5**, No. 7, pp. 1-196, pl. i.

1862b. Essai d'une Erpétologie de l'Algérie. Mém. Acad. Imp. Sci. St.-Pétersbourg, (7), **4**, No. 7, pp. 1-86.

1865. Die Vertheilung der Schildkröten über den Erdball. Ein zoogeographischer Versuch. Mém. Acad. Imp. Sci. St.-Pétersbourg, (7), **8**, No. 13, pp. 1-207.

1890. Bemerkungen über die Schildkrötensammlung im zoologischen Museum der kaiserlichen Akademie der Wissenschaften zu St.-

Petersburg. Mém. Acad. Imp. Sci. St.-Pétersbourg (7), **38**, No. 2, pp. 1-127, pls. i-iv.

TEMMINCK, C. J. and HERMANN SCHLEGEL

1835. Reptilia. *In* Ph. Fr. de Siebold, 1833-1838, Fauna Japonica. Leyden, xxi + 144 pp., pls. i-viii, map.

THOMSON, J. S.

1932. The Anatomy of the Tortoise. Sci. Proc. Royal Dublin Soc., (N.S.), **20**, pp. 359-461, pls. xix-xliii.

THUNBERG, C. P.

1795. Travels in Europe, Africa, and Asia, Made Between the Years 1770 and 1779. London, ed. 2, **1**, xxi + 317 pp. + Index, pls. i-ii; **2**, xvi + 316 pp. + Index, pls. i-iv.

TORNIER, GUSTAV

1896. Die Kriechthiere Deutsch-Ost-Afrikas. Beiträge zur Systematik und Descendenzlehre. Berlin. xiii + 164 pp. figs. 1-11, pls. i-v. (Reprinted in 1897.)

1897. Zur Faunistik Deutsch-Ost-Afrikas. III. Reptilien und Amphibien. Arch. Naturg., **63**, Abt. 1, pp. 63-66.

1898. Reptilien und Amphibien. *In* Werther, C. W., Die mittleren Hochländer des nördlichen Deutsch-Ost-Afrika. Berlin, pp. 281-304, figs. 1-15.

1900b. Neue Liste der Crocodile, Schildkröten und Eidechsen Deutsch-Ost-Afrikas. Zool. Jahrb., Syst. Abt., **13**, pp. 579-618, figs. A-H.

1901b. Die Reptilien und Amphibien der deutschen Tiefseeexpedition 1898/99. Zool. Anz., **24**, pp. 61-66.

1901c. Die Crocodile, Schildkröten und Eidechsen in Togo. Arch. Naturg., **67**, Festschrift vol., pp. 65-88.

1902b. Herpetologisch Neues aus Deutsch-Ost-Afrika. Zool. Jahrb., Syst. Abt., **15**, pp. 578-590, figs.

1902c. Die Crocodile, Schildkröten und Eidechsen in Kamerun. Zool. Jahrb., Syst. Abt., **15**, pp. 663-677, pl. xxxv.

1904b. Entstehen der Farbkleidmuster und Körperform der Schildkröten. Sitzungsb. Ges. Naturf. Freunde Berlin, pp. 297-307, pls. i-iii.

1905c. Schildkröten und Eidechsen aus Nordost-Afrika und Arabien. Zool. Jahrb., Syst. Abt., **22**, pp. 365-388.

TRIMEN, ROLAND

1893 and 1896. Reptiles and Amphibians. *In* Noble, John, Illustrated Handbook of the Cape and South Africa. London. (Herpetology is on pp. 78-88 of both 1st and 2nd editions.)

TRISTRAM, H. B.

1860. The Great Sahara: Wanderings South of the Atlas Mountains. London, App.; xiv + 435 pp., figs., pls. i-xi, maps 1-2. (The

herpetological list in the Appendix is a mere compilation of names, often misspelled, and *not* a reprint of his 1859 remarks in Proc. Zool. Soc. London, pp. 475-477 based on Günther's identifications.)

VAILLANT, LÉON

1880b. Sur la Disposition des Vertèbres cervicales chez les Chéloniens. Comptes Rendus Acad. Sci. (Paris), **91**, pp. 795-798.

1880c. Memoire sur la Disposition des Vertèbres cervicales chez les Chéloniens. Ann. Sci. Nat. (Paris), (6), **10**, art. 7, pp. 1-106, pls. xxvi-xxxi.

1886. Sur la Disposition du Tube digestif chez les Chéloniens (Première Note: Chéloniens herbivores). Bull. Soc. Philom. Paris, (7), **10**, pp. 135-138.

1889. Description d'une Tortue terrestre d'Espèce nouvelle (*Testudo yniphora*). Nouv. Arch. Mus. Hist. Nat. (Paris), (3), **1**, pp. 161-167, pls. xii-xv.

1904a. La Livrée néotésique de la Tortue sillonné (*Testudo calcarata* Schneider). Bull. Mus. Hist. Nat. (Paris), **10**, pp. 186-187, figs.

VILLIERS, ANDRÉ

1949. La Faune. *In* Encyclopédie coloniale et maritime Afrique Occidentale française. **2**, pp. 162-165, photos.

1950c. Reptiles. Ophidiens et Chéloniens. *In* Contribution à l'Etude de l'Air. Mém. Inst. Franc. Afrique noire, No. 10, pp. 337-344.

VINCIGUERRA, DECIO

1927. Risultati zoologici della Missione inviata dalla R. Società geografica italiana per l'Esplorazione dell'Oasi di Giarabub. Rettili, Batraci e Pesci. Ann. Mus. Civ. Stor. Nat. Genova, **52**, pp. 324-345.

WERNER, FRANZ

1892a. Ausbeute einer herpetologischen Excursion nach Ost-Algerien. Verh. Zool.-Bot. Ges. Wien, **42**, pp. 350-355.

1892b. Tierleben in Ost-Algerien. Zool. Garten, **33**, pp. 264-273.

1894. Zweiter Beitrag zur Herpetologie von Ost-Algerien. Verh. Zool. Bot. Ges. Wien, **44**, pp. 75-87.

1895c. Ueber sekundäre Geschlechtsunterschiede bei Reptilien. Biol. Centralbl. (Leipzig), **15**, pp. 125-140.

1898a. Ueber Reptilien und Batrachier aus Togoland, Kamerun und Tunis aus dem kgl. Museum für Naturkunde in Berlin. II. Verh. Zool.-Bot. Ges. Wien, **48**, pp. 191-213, figs., pl. ii.

1902a. Ueber westafrikanische Reptilien. Verh. Zool.-Bot. Ges. Wien, **52**, pp. 332-348.

1908. (1907) Ergebnisse der mit Subvention aus der Erbschaft Treitl unternommen zoologischen Forschungsreise Dr. Franz Werner's nach

dem ägyptischen Sudan und Nord-Uganda. XII. Die Reptilien und Amphibien. Sitzungsb. Akad. Wiss. Wien, **116**, Abt. I, pp. 1823-1926, pls. i-iv.

1908a. On Some Interesting Reptiles Collected by Dr. C. M. Wenyon on the Upper Nile. Third Rep. Wellcome Trop. Res. Lab. Khartoum, pp. 169-172, fig. 42, pls. xvii-xx.

1909a. Reptilien, Batrachier und Fische von Tripolis und Barka. Zool. Jahrb., Syst. Abt., **27**, pp. 596-646, pl. xxx.

1910a. Reptilia et Amphibia. *In* Schultz, L., Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika. IV. Denkschr. Med.-Nat. Ges. Jena, **16**, pp. 279-370, figs. 1-15.

1912b. Die Lurche und Kriechtiere. *In* Brehm, A., Tierleben. Leipzig, ed. 4, **4**, xiv + 572 pp., figs., pls. maps.

1913d. Neue oder seltene Reptilien und Frösche des naturhistorischen Museums in Hamburg. Mitt. Nat. Mus. Hamburg, **30**, pp. 1-51.

1914b. Ergebnisse einer von Prof. F. Werner im Sommer 1910 mit Unterstützung aus dem Legate Wedl ausgeführten zoologischen Forschungsreise nach Algerien. II. Vertebrata. (a) Reptilien und Batrachier. Sitzungsb. Akad. Wiss. Wien, **123**, Abt. I, pp. 331-358, pl.

1915. Reptilia und Amphibia. *In* Michaelsen, W., Beiträge zur Kenntnis der Land- und Süsswasserfauna Deutsch-Südwestafrikas. III. Hamburg, pp. 325-376, pl. vii.

1920. Edition 5 of 1912b.

1924a. Wissenschaftliche Ergebnisse der mit Unterstützung der Akademie der Wissenschaften in Wien aus der Erbschaft Treitl von F. Werner unternommenen zoologischen Expedition nach dem anglo-ägyptischen Sudan (Kordofan) 1914. XVIII. Schildkröten. Denkschr. Akad. Wiss. Wien, **99**, pp. 263-273, figs.

1929b. Wissenschaftliche Ergebnisse einer zoologischen Forschungsreise nach Westalgerien und Marokko. Sitzungsb. Akad. Wiss. Wien, **138**, Abt. I, pp. 1-34, fig. 1, pls. i-iv.

1931c. Ergebnisse einer zoologischen Forschungsreise nach Marokko. III. Amphibien und Reptilien. Sitzungsb. Akad. Wiss. Wien, **140**, Abt. I, pp. 271-318, pls. i-iv, maps 1-3.

WETTSTEIN, OTTO

1924. Über *Testudo tornieri* Siebr. und *Testudo loveridgii* Blgr. Zool. Anz., **61**, pp. 201-208, figs. 1-2.

WILLIAMS, E. E.

1950. Variation and Selection in the Cervical Central Articulation of Living Tortoises. Bull. Amer. Mus. Nat. Hist., **94**, pp. 507-561.

1952. A New Fossil Tortoise from Mona Island, West Indies, and a

Tentative Arrangement of the Tortoises of the World. Bull Amer. Mus. Nat. Hist., **99**, pp. 543-560.

WILLIAMS, E. E. and S. B. MCDOWELL

1952. The Plastron of Soft-shelled Turtles (Testudinata: Trionychidae): a new Interpretation. Jour. Morph., **90**, pp. 263-280, pls. i-ii.

WITTE, G. F. DE

1924d. Deux Tortues à Squelette réduit. Revue Zool. Afr., **12**, Suppl., p. 48.

1928b. Les Tortues *Trionyx* du Lac Albert. Revue Zool. Afr., **15**, Suppl., p. 49.

1932d. Un Tortue marine. Revue Zool. Bot. Afr., **22**, Suppl., p. 57.

1933m. Reptiles récoltés au Congo belge par le Dr. H. Schouteden et par M. G.-F. de Witte. Ann. Mus. Congo belge, Zool., (1), **3**, pp. 55-98, pls. i-iv.

1935. Un Tortue marine de Banana. Revue Zool. Bot. Afr., **27**, Suppl., p. 94.

1941. Exploration du Parc National Albert. Mission G. F. de Witte (1933-1935). Batraciens et Reptiles. Inst. Parcs Nat. Congo belge, Fasc. 33, xviii + 261 pp., figs. 1-50, pls. i-xlvi, map.

1952. Amphibiens et Reptiles. *In* Exploration Hydrobiologique du Lac Tanganyika (1946-1947). **3**, Fasc. 3, pp. 1-22, pl. i.

1953. Exploration du Parc National de l'Upemba. Mission G. F. de Witte en collaboration avec W. Adam, A. Janssens, L. van Meel et R. Verheyen (1946-1949). Reptiles. Inst. Parcs Nat. Congo belge, Fasc. 6, pp. 1-322, figs. 1-111, pls. i-xli, map.

WORTHINGTON, E. B.

1929. A Report on the Fishing Survey of Lakes Albert and Kioga. Cambridge, Eng., pp. 1-136.

WORTHINGTON, S. and E. B.

1933. Inland Waters of Africa. London, ix + 259 pp., figs. 1-13, pls. i-xi, map.

WYMAN, JEFFRIES

1845. Exhibition of "Shell of *Kinixys homeana*, Bell, from Cape de Verd Islands." Proc. Boston Soc. Nat. Hist., **2**, p. 38.

ZANGERL, RAINER

1939. The Homology of the Shell Elements in Turtles. Jour. Morph., **65**, pp. 383-406, figs. 1-9, pls. i-ii.

ZAVATTARI, EDOARDO

1922. Vertebrati di Cirenaica raccolti dal Generale Medico Prof.
(1924) Francesco Testi. Atti. Soc. Nat. Modena, (6), **1**, pp. 13-22.

1929. Elenco degli Anfibi e Rettili della Cirenaica. Notiziario Economico della Cirenaica (Bengasi), pp. 86-88.

1930a. Erpetologia della Cirenaica. Arch. Zool. Ital. (Torino), **14**, pp. 253-287.

1937. I Vertebrati della Libia. *In* Festschrift zum 60. Geburtstage von Professor Dr. Embrik Strand. Riga, **2**, pp. 526-560.

ZULUETA, ANTONIO DE

1908. Nota sobre Batracios y Reptilos de Mogador, con Descripcion de la Forma joven de *Saurodactylus mauritanicus* (Dum. et Bibr.). Bol. Real Soc. Esp. Hist. Nat. (Madrid), **8**, pp. 451-457.

INDEX TO ALL SCIENTIFIC NAMES[1]

Achilemys, 219.
Achinixys, 218, 259, 296, 297, 343, 377.
Acinixys planicauda, *217*.
Aegyptiacum, Hyalomma, 273.
aegyptiacus, Aspidonectes, 424.
aegyptiacus, Gymnopus, 424.
aegyptiacus, Trionyx, 420, 422, 423.
africana, Fordia, 421, 425.
africana, Testudo, 368, 369.
africana, Testudo t., 345, 346.
agassizii, Chelonia, 475.
agassizii, Gopherus, *186*.
alata, Mutela, 466.
albanica, Chersinella t., 301, 337, 339.
albanica, Psammobates t., 337.
Aldabrachelys, 166, 223, **225**.
Aldabrachelys gigantea, 225.
Aldabrachelys grandidieri, 225.
Aldabrachelys sumeiri, 225.
aldabrensis, Fregatta m., 480.
amasensis, Chersinella v., 301, 327.
Amblyomma exornatum, 248.
Amblyomma marmoreum, 248, 293, 393.
Amblyomma nuttalli, 248, 293, 393.
amboinensis, Testudo m., 319.
Amyda, 421, 422.
Amyda mutica, 422.
Amyda subplana, 422.
Amyda triunguis, 426.
Amyda t. triunguis, 427.
angulata, Chersina, 167, 212, 344, **345-352**, *212*, *214*, *217*, *344*, *347*, *349*.
angulata, Chersine, 346.
angulata, Neotestudo, 346.
angulata, Testudo, 342, 345, 346.
angulata, Testudo (C.) 346.
angulatus, Goniochersus, 346.
angusta, Sphargis, 500.
Annamemys, 187, 188.
antiguorum, Emys, 202.
arachnoides, Pyxis, 259, 364, *217*.
aralensis, Emys o., 204.
arcuata, Testudo, 499.
Ardea c. cinerea, 480.
areolata, Chersine, 368.
areolata, Testudo, 352, 367, 369, 387.
areolatus, Homopus, 173, 353, 355-360, **367-374**, 378, *215*, *222*, *357*, *358*, *370*, *372*.
armata, Testudo, 251.
Aspideretes, 422.
Aspidochelys, 452.
Aspidochelys livingstonii, 452, 459, 460.
Aspidonectes, 420.
Aspidonectes, 424.
Aspidonectes aspilus, 425.
Aspilus, 421.
aspilus, Aspidonectes, 425.
aspilus, Gymnopus, 426.
Asterochelys, 223.
Asterochelys yniphora, 224.
Astrorchis renicapite, 502.
atlantica, Dermochelis, 500.
astra, Caretta, 490.
atra, Halichelys, 489.
aubryi, Cryptopodus, 453.
aubryi, Cryptopus, 452.
aubryi, Cycloderma, 168, 417-420, **453-459**, 460, 468, *456*, *458*.
aubryi, Heptathyra, 453.

[1] Misprints such as *Cinicys, Cininixys, Homoeopus, Tistudo*, etc., are not included. The pagination of a valid name's main discussion is indicated by boldface type. All synonyms are indexed. Pages on which illustrations and maps occur are cited in italics after the other page references.

australis, Kinixys, 387.
australis, Kinixys a., 388.
babcocki, Geochelone p., 167-169, 227-231, **235-251**, 252, 299, 360, *212*, *214*, *217*, *226*, *234*, *239*, *257*, *267*.
Baikia, 436.
Baikiea, 436.
Baikiea elegans, 436-438, 444.
baikii, Tetrathyra, 438, 439, 443, 444.
bealei, Cistuda, 191.
Bellemys, 218.
belliana, Cinixys, 286, 287, 385, 396.
belliana, Cinothorax, 385.
belliana, Kinixys, 166, 374, 377-380, 383, 384, 388, 396, 404.
belliana, Kinixys b., 167, 287, 289, 292, 321, 369, 376, 383, **384-396**, 397, *215*, *219*, *379*, *389*.
bellii, Testudo, 346.
bergeri, Chersinella v., 327.
bergeri, Homopus, 289, 296, 299, 301, 309, 310, 326, 330, 331, 358, 362.
bergeri, Testudo, 326.
bergeri, Testudo v., 327.
bergiana, Eragrostris, 341.
bettai, Testudo g., 265.
bibronii, Pelochelys, 415.
bicarinata, Chelonia, 474.
bicinctum, Cinctisternum, 422.
biguttata, Testudo, 229, 250, 251.
bipunctata, Testudo, 229, 251.
bissa, Caretta, 485, 488.
blandingii, Cistuda, 189.
blandingii, Emydoidea, 167, 188, 189.
blandingii, Emys, 184.
boettgeri, Chersinella, 327.
boettgeri, Chersinella v., 327.
boettgeri, Testudo, 299, 301 326, 327, 329, 330, 332.
boulengeri Chersobius, 362.
boulengeri, Homopus, 168, 326, 354 359, **362-365**, 378, *215*, *219*, *357*, *358*, *363*.
boulengeri, Pseudomopus, 362.
Bulbine caulescens, 367.
Caelatura nyassensis, 466.
cafra, Testudo, 360.
cafra, Testudo c., 360.
calcarata, Chersine, 231.
calcarata, Testudo, 228, 231, 238, 241.
Calemys, 191.
Callagur, 187.
Callinia, 421.
callosa, Cyclanosteus s., 438, 444.
Camallanus microcephalus, 199.
campanulata, Testudo, 264, 277.
Caouana, 489.
Caouana caretta, 491.
caouana, Chelonia, 491.
Caouana dessumierii, 495.
Caouana elongata, 491.
Caouana olivacea, 495.
Caouana ruppellii, 495.
caouana, Testudo, 490.
caouana, Thalassochelys, 489.
Caretta, 469, 470, 484, **489-490**.
Caretta atra, 490.
Caretta bissa, 485, 488.
Caretta caretta, 471, **490-494**.
Caretta c. caretta, 492.
Caretta c. gigas, 492.
Caretta c. olivacea, 496.
Caretta esculenta, 474.
Caretta gigas, 492, 493.
Caretta imbricata, 485.
Caretta nasicornis, 474.
Caretta nasuta, 489, 490.
Caretta olivacea, 495.
Caretta remivaga, 495.
Caretta rostrata, 486.

Caretta squamosa, 485.
Caretta thunbergii, 474.
caretta, Caouana, 491.
caretta, Caretta, 471, **490-494**.
caretta, Caretta c., 492.
caretta, Testudo, 470, 489, 490.
caretta, Thalassochelys, 491, 495.
cariniferus, Trionyx, 421.
Carteremys, 277.
cartilaginea, Testudo, 421.
cartilagineus, Trionyx, 415.
caspica, Clemmys, 192, 195.
caspica, Emys, 193.
caspica, Testudo, 191.
castanea, Kinixys, 374, 401, 405.
caulescens, Bulbine, 367.
Centrochelys, 221.
Centrochelys (P.) sulcatus, 231.
cepediana, Testudo, 474.
cephalo, Testudo, 489, 490.
Cephalochelys, 489.
Cephalochelys oceanica, 489, 491.
Ceramopelta, 422.
Ceramopelta latirostris, 422.
Chamaerops humilis, 275.
Cheirogaster, 219.
Chelona, 473.
Chelone, 473.
Chelone imbricata, **486**.
Chelone midas, 476.
Chelone mydas, 475.
Chelone virgata, 476.
Chelone viridis, 475.
Chelonia, **472-473**.
Chelonia agassizii, 475.
Chelonia bicarinata, 474.
Chelonia caouana, 491.
Chelonia corticata, 491.
Chelonia depressa, 469, 475.
Chelonia dubia, 495.
Chelonia dussumieri, 495.
Chelonia formosa, 475.
Chelonia imbricata, 485.
Chelonia lachrymata, 474.
Chelonia lata, 475.
Chelonia lutaria, 499.
Chelonia maculosa, 474.
Chelonia marmorata, 474.
Chelonia midas, 475.
Chelonia multiscutata, 495.
Chelonia mydas, 469, 471, **474-485**.
Chelonia m. japonica, 476.
Chelonia m. mydas, 476.
Chelonia olivacea, 494, 495.
Chelonia pelasgorum, 490.
Chelonia polyaspis, 495.
Chelonia pseudocaretta, 485.
Chelonia pseudomydas, 485.
Chelonia tenuis, 475.
Chelonia virgata, 474.
Chelonia viridis, 474.
Cheloniidae, 180, 468, 472.
Chelonoidis, 223.
Chelopus, 191.
Chelydra, 189.
Chelyra, 499.
Chersina, 218, 220, 255, 259, 296, 297, **342-345**, 346, 377, 378.
Chersina angulata, 167, 344, **345-352**, *212*, *214*, *217*, *344*, *347*, *349*.
Chersine, 254, 346.
Chersine angulata, 346.
Chersine areolata, 368.
Chersine calarata, 231.
Chersine geometrica, 321.
Chersine pusilla, 345.
Chersine signata, 360.
Chersine tetradactyla, 368.
Chersinella, 254, 294, 299.
Chersinella boettgeri, 327.
Chersinella fiski, 326, 327.
Chersinella f. colesbergensis, 301, 326.
Chersinella f. cronwrighti, 301, 326.
Chersinella f. grica, 301, 327.
Chersinella f. gricoides, 301, 327.

Chersinella f. orangensis, 301, 326.
Chersinella f. seimundi, 326.
Chersinella geometrica, 321.
Chersinella graeca, 264.
Chersinella oculifera, 316.
Chersinella schonlandi, 301, 307, 309, 310, 311, 326, 329.
Chersinella strauchi, 321.
Chersinella tentoria, 337.
Chersinella t. albanica, 301, 337, 339.
Chersinella t. duerdeni, 301, 337.
Chersinella t. hexensis, 301, 309, 333, 338.
Chersinella t. karuella, 301, 337, 339.
Chersinella t. karuica, 301, 337.
Chersinella t. lativittata, 301, 337.
Chersinella t. piscatella, 301, 337.
Chersinella t. subsulcata, 301, 337.
Chersinella t. tentorioides, 301, 337.
Chersinella trimeni, 333.
Chersinella verroxii, 327.
Chersinella v. amasensis, 301, 327.
Chersinella v. bergeri, 327.
Chersinella v. boettgeri, 327.
Chersinella v. smithi, 327.
Chersobius, 352, 355, 360.
Chersobius boulengeri, 362.
Chersobius signatus, 360.
Chersus, 254.
Chersus mauritanicus, 264, 276.
Chilensis, Geochelone, 235.
Chitra, 414, 417.
Chitra indica, 415.
Chrysemys, 187.
Cinctisternum, 422.
Cinctisternum bicinctum, 422.
cinerea, Ardea c., 480.
Cinixys, 374.
Cinixys belliana, 286, 287, 385, 396.
Cinixys dorri, 397.
Cinixys homeana, 400.
Cinixys lobatsiana, 387, 389, 394.
Cinixys nogueyi, 397.
Cinothorax, 374, 378, 379.
Cinothorax belliana, 385.
Cissus, 248.
Cistuda bealei, 191.
Cistuda blandingii, 189.
Cistuda hellenica, 203.
Cistudo europaea, 203.
Cistudo lutaria, 203.
Clemmys, 187, 189, **191**, 205, 209.
Clemmys caspica, 192, 195.
Clemmys c. caspica, 192.
Clemmys c. cretica, 192.
Clemmys c. leprosa, 190, **192-201**, 204, *170, 190, 196, 212, 214, 217*.
Clemmys c. rivulata, 192.
Clemmys c. sigriz, 195.
Clemmys fuliginosa, 194.
Clemmys laticeps, 193.
Clemmys leprosa, 193.
Clemmys marmorea, 193.
Clemmys oculifera, 316.
Clemmys sigriz, 193.
Coelognathus, 422.
Coelognathus novemcostatus, 422.
colesbergensis, Chersinella f., 301, 326.
colesbergensis, Psammobates f., 327.
Colpochelys, 494.
Colpochelys kempi, 494.
comptoni, Emys, 353, 354.
comptoni, Testudo, 218, 354.
contortus, Spiroxys, 199.
controversa, Thalassochelys, 495.
Coptopelta, 422.
Coptopelta septemcostata, 422.
coriacea, Dermatochelys, 500.
coriacea, Dermochelis, 500.
coriacea, Dermochelys, 469, 471, *499-503*.
coriacea, Dermochelys c., 500.

coriacea, Sphargis, 500.
coriacea, Testudo, 499.
Coriudo, 499.
corticata, Chelonia, 491.
corticata, Thalassochelys, 491, 492.
costaricensis, Geochelone, 224.
Crassulaceae, 331.
cretica, Clemmys c., 192.
cronwrighti, Chersinella f., 301, 326.
cronwrighti, Psammobates f., 327.
Cryptodira, 180.
Cryptopodus, 452.
Cryptopodus aubryi, 453.
Cryptopus, 452.
Cryptopus aubryi, 452.
Cryptopus senegalensis, 443.
Cuora, 188.
Cyclanorbis, 414, 417, 420, 435, ***436-438***, 451, 452.
Cyclanorbis elegans, 167, 417-420, 436, 437, **438-443**, 444, 449, *419*, *440*, *441*.
Cyclanorbis oligotylus, 167, 437, 438, 443.
Cyclanorbis petersii, 436, 443.
Cyclanorbis senegalensis, 417-420, 436-439, **443-450**, 451, *419*, *445*, *447*.
Cyclanorbis sp., 450-451.
Cyclanosteus, 436.
Cyclanosteus frenatus, 459.
Cyclanosteus petersii, 436, 443.
Cyclanosteus senegalensis, 438, 443.
Cyclanosteus s. callosa, 438, 444.
Cyclanosteus s. equilifera, 444.
Cyclanosteus s. normalis, 444.
Cyclemys, 188.
Cyclemys mouhoti, 183.
Cycloderma, 166, 414, 417, 420, 436, **451-453**, 467.
Cycloderma aubryi, 168, 417-420, **453-459**, 460, 468, *456*, *458*.
Cycloderma frenatum, 173, 417-420, 451-453, 455, **459-468**, *461*, *463*.
Cycloderma petersii, 443.
Cycloderma senegalense, 443.
Cylindraspis, 223, 224.
Cypraea moneta, 323.
Damonia, 187.
darlingi, Homopus, 296, 387.
darlingi, Kinixys, 387.
Deirochelys, 187, 188.
Deirochelys reticularia, 184, 188, 189.
denticulata, Geochelone, 255.
denticulata, Kinixys, 407.
denticulata, Testudo, 404.
depressa, Chelonia, 469, 475.
depressa, Gari, 494.
depressa, Psammobates, 301, 327, 329, 331.
Dermatochelys, 499.
Dermatochelys coriacea, 500.
Dermatochelys porcata, 500.
Dermochelis, 499.
Dermochelis atlantica, 500.
Dermochelis coriacea, 500.
Dermochelyidae, 180, 468, **498**.
Dermochelys, **499**.
Dermochelys coriacea, 469, 471, **499-503**.
Dermochelys c. coriacea, 500.
Dermochelys c. schlegelii, 500.
dessumierii, Caouana, 495.
Diosma, 323.
Diosma pulchella, 323.
Dogania, 421, 422.
Dogania subplana, 415.
dorri, Cinixys, 397.
dubia, Chelonia, 495.
ductor, Echeneis, 502.
duerdeni, Chersinella t., 301, 337.
duerdeni, Psammobates t., 338.
dussumieri, Chelonia, 495.
Echeneis, ductor, 502.

Echeneis naucrates, 481.
Echweria, 273.
elegans, Baikiea, 436-438, 444.
elegans, Cyclanorbis, 167, 417-420, 436, 437, **438-443**, 444, 449, *419*, *440*, *441*.
elegans, Geochelone, 226, 255, 299.
elegans, Testudo, 221, 225.
ellipticus, Lanistes, 466.
elongata, Cauoana, 491.
elongata Eremonia, 489.
Emmenia, 191.
emoryi, Trionyx, 417.
Emyda senegalensis, 443.
Emydinae, 182, **183-189**, 190, 375, *185*.
Emydoidea, 167, 187, 188, **189**, 299.
Emydoidea blandingii, 167, 188, 189.
Emys, 167, 184, 188, **201-202**, 299.
Emys antiguorum, 202.
Emys blandingii, 184.
Emys caspica, 193.
Emys caspia var. leprosa, 195.
Emys comptoni, 353, 354.
Emys europaea, 203.
Emys flavipes, 195.
Emys fraseri, 195.
Emys fuliginosus, 191, 193.
Emys grayi, 191.
Emys hellenica, 203.
Emys hofmani, 203.
Emys iberica, 203.
Emys lamaria, 195.
Emys laniaria, 195.
Emys laticeps, 191, 193.
Emys leprosa, 191, 192.
Emys lutaria, 193, 203, 204.
Emys marmorea, 192.
Emys oculifera, 316.
Emys orbicularis, 167, 170, 184, 188, 191, 201, **202-209**, *190*, *205*, *206*, *212*, *214*, *217*.
Emys o. aralensis, 204.
Emys o. hellenica, 204.
Emys o. orbicularis, 204.
Emys scutella, 353.
Emys sigriz, 193.
Emys vulgaris, 193.
emys, Geochelone, 224, 255.
equlifera, Cyclanosteus s., 444.
Eragrostris bergiana, 341.
Eremonia, 489.
Eremonia elongata, 489.
Eretmochelys, **484-485**.
Eretmochelys imbricata, 469, 471, **485-489**.
Eretmochelys i. imbricata, 486.
Eretmochelys i. squamosa, 486.
Eretmochelys squamata, 485.
erosa, Kinixys, 230, 377-381, 383, 384, 403, **404-411**, *215*, *217*, *257*, *377*, *379*, *380*, *381*, *408*, *409*.
erosa, Testudo, 374, 404.
Eryma, 191.
Eryma laticeps, 195.
esculenta, Caretta, 474.
Euamyda, 422.
Euchelonia, 473.
Euchelys, 473.
Euchelys macropus, 473, 477.
euphratica, Testudo, 421.
euphraticus, Trionyx, 417.
europaea, Cistudo, 203.
europaea, Emys, 203.
europaea, Lutremys, 203.
europaea, Testudo, 201, 202.
exornatum, Amblyomma, 248.
Falcaustra lambdiensis, 199.
fasciata, Testudo, 369.
femoralis, Homopus, 168, 355-359, **365-367**, 378, *357*, *358*.
ferox, Testudo, 421.
ferox, Trionyx, 417.
fiski, Chersinella, 326.
nski, Testudo, 295, 301, 325, 326-

329, 331.
fiskii Psammobates, 327.
fiskii, Psammobates f., 327.
fiskii, Testudo t., 326, 333.
flava, Testudo, 202.
flavipes Emys, 195.
floweri, Testudo g., 259, 260.
Fordia, 421.
Fordia africana, 421, 425.
formosa, Chelonia, 475.
formosus, Trionyx, 415, 421.
fraseri, Emys, 195.
Fregatta m. aldabrensis, 480.
frenata, Heptathyra, 454, 459.
frenatum, Cycloderma, 173, 417-420, 451-453, 455, **459-468**, *461*, *463*.
frenatus, Cyclanosteus, 459.
fuliginosa, Clemmys, 194.
fuliginosa, Mauremys, 194.
fuliginosus, Emys, 191, 193.
gabonensis, Pelusios, 453.
gangeticus, Trionyx, 415, 422.
Gari depressa, 494.
Geochelone, 165, 218, 220, **221-225**, **225-230**, 238, 255, 256, 284, 293-295, 299, 342, 343, 344, 354, 355, 378.
Geochelone costaricensis, 224.
Geochelone denticulata, 255.
Geochelone elegans, 226, 255, 299.
Geochelone emys, 224, 255.
Geochelone, gigantea, 225, 255, 295.
Geochelone grandidieri, 224, 225.
Geochelone kaiseni, 224.
Geochelone nana, 224.
Geochelone pardalis, 224, 227, 238, 251, 254, 255.
Geochelone p. babcocki, 167-169, 225, 227-231, 234, **235-251**, 252, 254, 299, 360, *212 214*, *217*, *226*, *234*, *239*, *257*, *267*.
Geochelone p. pardalis, 227-230, 250, **251-254**.
Geochelone platynota, 226.
Geochelone radiata, 224.
Geochelone senegalensis, 231.
Geochelone sulcata, 168, 225-229, **230-235**, 241, 247, 369, *226*, *232*.
Geochelone sumeiri, 225, 259.
Geochelone uintensis, 224.
Geochelone yniphora, 342.
Geoclemmys, 191.
Geoemyda, 187.
Geoemyda punctularia, 350.
geographicus, Peltastes, 321.
geometrica, Chersine, 321.
geometrica, Chersinella, 321.
geometrica, Testudo, 173, 201, 294, 299, 301, 316, 319, 323, 337, 387.
geometricus group, 295, 296, 298, 299, 301, 303, 326.
geometricus Peltastes, 321.
geometricus, Psammobates, 168, 174, 253, 291, 300-303, 314, 316, **319-324**, *313*.
gigantea, Aldabrachelys, 225.
gigantea, Geochelone, 225, 255, 295.
gigas, Caretta, 492, 493.
gigas, Caretta c., 492.
Glossiphonidae, 466.
Glyptemys, 191.
Gomphopelta, 421.
Gomphopelta officinalis, 421.
Goniochersus, 342.
Goniochersus angulatus, 346.
Gopherus, 218, 255, 256, 295, 343, 355.
Gopherus agassizii, *186*.
Gopherus polyphemus, 283.
graeca, Chersinella, 264.
graeca, Testudo, 170, 218, 254-256, 258, 259, 261, 276, 282, 298, 299.
graeca, Testudo g., 259, 260, **261-276**, *212*, *214*, *217*, *257*, *266*, *267*.
grandidieri, Aldabrachelys, 225.

grandidieri, Geochelone, 224, 225.
Graptemys, 187.
grayi, Emys, 191.
grica, Chersinella f., 301, 327.
gricoides, Chersinella f., 301, 327.
guttata, Testudo, 191.
Gymnopus, 420.
Gymnopus aegyptiacus, 424.
Gymnopus aspilus, 426.
Hadrianus, 218, 222-224, 355.
Halichelys, 489.
Halichelys atra, 489.
hellenica, Cistuda, 203.
hellenica, Emys, 203.
hellenica, Emys o., 204.
Heptathyra, 452.
Heptathyra aubryi, 453.
Heptathyra frenata, 454, 459.
Heptathyra livingstonii, 459.
hermanni, Testudo, 170, 258, 260, 265, 281, *212*, *257*, *281*.
Herpysmostes, 484.
Hesperotestudo, 223, 224.
hexensis, Chersinella t., 301, 309, 333, 338.
Hieremys, 298.
hofmani, Emys, 203.
homeana, Cinixys, 400, 404.
homeana, Kinixys, 377-381, 383, 384, 399, **400-404**, *215*, *379*, *380*, *381*, *401*.
Homopus, 218, 221, 255, 259, 284, 295-297, 328, 343, 344, **352-359**, 360, 377, 378.
Homopus areolatus 173, 353, 355-360, **367-374**, 378, *215*, *222*, *357*, *358*, *370*, *372*.
Homopus bergeri, 289, 296, 299, 301, 309, 310, 326, 330, 331, 358, 362.
Homopus boulengeri, 168, 326, 354-359, **362-365**, 378, *215*, *219*, *357*, *358*, *363*.
Homopus darlingi, 296, 387.
Homopus femoralis, 168, 355-359, **365-367**, 378, *357*, *358*.
Homopus nogueyi, 296, 397.
Homopus signatus, 168, 173, 237, 316, 353-357, **359-362**, 369, 378, *217*, *357*, *358*.
horsfieldi, Testudo, 254, 258, 283.
humilis, Chamaerops, 275.
hurum, Trionyx, 415.
Hyalomma aegyptiacum, 273.
Hyalomma syriacum, 273.
Hydrone, 201.
ibera, Testudo, 170, 262, 265.
ibera, Testudo g., 259, 265.
iberica Emys, 203.
Ida, 421.
imbricata, Caretta, 485.
imbricata, Chelone, 486.
imbricata, Chelonia, 485.
imbricata, Eretmochelys, 469, 471, **485-489**.
imbricata, Eretmochelys i., 486.
imbricata, Testudo, 484, 485.
indica, Chitra, 415.
Indotestudo, 223, 224.
insculpta Clemmys, *186*.
insculpta, Testudo, 191.
irrorata, Landemania, 421.
Isola, 421.
jaegerskioeldi, Placobdella, 466.
japonica, Chelonia m., 476.
japonica, Testudo, 474.
javanicus, Trionyx, 421.
jordani, Kinixys, 387.
jujuba, Zizyphus, 275.
kaiseni, Geochelone, 224.
karuella, Chersinella t., 301, 337, 339.
karruica, Psammobates t., 338.
karuica, Chersinella t., 301, 337.
kempi, Colpochelys, 494.
kempi, Lepidochelys o., 496, 497.

Kinixys, 166, 218, 220, 259, 288, 296, 342-344, **374-384**.
Kinixys australis, 387.
Kinixys a. australis, 388.
Kinixys a. mababiensis, 388.
Kinixys belliana, 166, 374, 377-380, 383, 384, 388, 396, 404.
Kinixys b. belliana, 167, 287, 289, 292, 321, 368, 369, 376, 383, **384-396**, 397, *215*, *219*, *379*, *389*.
Kinixys b. nogueyi, 166, 383, 388, **396-399**, *380*, *381*.
Kinixys b. spekei, 388.
Kinixys b. zombensis, 387.
Kinixys b. zuluensis, 387.
Kinixys castanea, 374, 401, 405.
Kinixys darlingi, 387.
Kinixys denticulata, 407.
Kinixys erosa, 230, 377-381, 383, 384, 403, **404-411**, *215*, *217*, *257*, *377*, *379*, *380*, *381*, *408*, *409*.
Kinixys homeana, 377-381, 383, 384, 399, **400-404**, *215*, *379*, *380*, *381*, *401*.
Kinixys jordani, 387.
Kinixys lobatsiana, 388, 389.
Kinixys natalensis, 388, 390.
Kinixys nogueyi, 397.
Kinixys schoensis, 387.
Kinixys spekii, 379, 380, 387, 391.
Kinixys youngi, 388.
Kinixys zombensis, 388.
Kinixys zuluensis, 388.
Kinothorax, 374.
kleinmanni, Pseudotestudo, 276.
kleinmanni, Testudo, 218, 220, 258-261, 264, **276-283**, *212*, *214*, *278*, *279*, *280*.
kraussi, Onychochelys, 484, 486.
labiatus, Trionyx, 424, 427, 433, 434.
Lacerta, 275.
lachrymata, Chelonia, 474.
laevis, Psilognathus, 421.
lamaria, Emys, 195.
lambdiensis, Falcaustra, 199.
Landemania, 421.
Landemania irrorata, 421.
laniaria, Emys, 195.
laniaria, Mauremys, 194.
Lanistes ellipticus, 466.
Lanistes sordidus, 466.
lata, Chelonia, 475.
laticeps, Clemmys, 193.
laticeps, Emys, 191, 193.
laticeps Eryma, 195.
latirostris, Ceramopelta, 422.
lativittata, Chersinella t., 301, 337.
leithii, Peltastes, 277.
leithii, Testudo, 218, 276, 277, 280.
leithii, Trionyx, 415.
Lepidochelys, 469, 470, **494-495**.
Lepidochelys olivacea, 494.
Lepidochelys o. kempi, 496, 497.
Lepidochelys o. olivacea, 471, **495-498**.
leprosa, Clemmys, 193.
leprosa, Clemmys c., 190, **192-201**, 204, *170*, *190*, *196*, *212*, *214*, *217*.
leprosa, Emys, 191, 192.
leprosa, Emys c., 195.
leprosus, Yuen, 421.
Limonium, 282.
Lissemys, 412, 414, 415, 417.
livingstonii, Aspidochelys, 452, 459, 460.
livingstonii, Heptathyra, 459.
lobatsiana, Cinixys, 387, 389, 394.
lobatsiana, Kinixys, 388.
Lorica t. signatae, 359.
loveridgii, Testudo, 287-290, 292, 387.
lutaria, Chelonia, 499.
lutaria, Cistudo, 203.
lutaria, Emys, 193, 203, 204.
lutaria, Testudo, 201, 202.

luteola, Testudo, 253, 299, 301, 321, 323.
Lutremys, 201.
Lutremys europaea, 203.
lyra, Testudo, 499.
mababiensis, Kinixys a., 388.
macropus, Euchelys, 473, 477.
macropus, Testudo, 474.
maculosa, Chelonia, 474.
Malaclemys, 187.
Malacochersus, 165, 166, 219, 220, 255, 257, **283-286**, 289, 296, 343, 378, 394.
Malacochersus procterae, 287, *285*.
Malacochersus tornieri, 167, 172, 284, **286-294**, 378, 388, *212*, *214*, *217*, *257*, *285*, *288*.
Manouria, 223, 224.
marginata, Testudo, 173, 254, 258, 261, 262, 264, 276, 282.
marina, Testudo, 474.
marmorata, Chelonia, 474.
marmorea, Clemmys, 193.
marmorea, Emys, 192.
marmoreum, Amblyomma, 248, 293, 393.
Mauremys, 191.
Mauremys fuliginosa, 194.
Mauremys laniaria, 194.
mauritanica, Testudo, 262.
mauritanica, Testudo g., 264.
mauritanicus, Chersus, 276.
Medaestia, 254.
Megachersine, 221.
Megachersine pardalis, 238.
Megalochelys, 223, 224.
Megemys, 473.
Melanemys, 191.
meleagris, Testudo, 202.
mercuralis, Sphargis, 499.
Mesembryanthemum, 332.
microcephalus, Camellanus, 199.
midas, Chelone, 476.
midas, Chelonia, 475.
miniata, Testudo, 368, 369.
minuta, Testudo, 323.
Monachelys, 223.
moneta, Cypraea, 323.
mordax, Temnognathus, 421.
Morenia, 187.
mortoni, Trionyx, 425.
moubata, Ornithodorus, 332.
mouhoti, Cyclemys, 183.
mouhoti, Pyxidea, 183.
muhlenbergii, Testudo, 191.
multiscutata, Chelonia, 495.
Mutela alata,466.
mutica, Amyda, 422.
muticus, Trionyx, 417.
Mydas, 473.
Mydas viridis, 475.
mydas, Chelone, 475.
mydas, Chelonia, 469, 471, **474-485**.
mydas, Chelonia m., 476.
mydas, Testudo, 473, 474.
Mydasea, 473.
nana, Geochelone, 224.
Nanemys, 191.
nasicornis, Caretta, 474.
nasicornis, Testudo, 490.
nasuta, Caretta, 489, 490.
natalensis, Kinixys, 388, 390.
Natator tessellatus, 475.
nauerates, Echeneis, 481.
nebrascensis, Stylemys, 256.
Neoemys, 189.
Neotestudo, 342.
Neotestudo angulata, 346.
niger, Pelusios, 453.
nigricans, Trionyx, 415.
nigrita, Xylocopa, 392.
nigriventris, Testudo g., 301, 337.
nilotica, Tyrse, 425.
niloticus, Trionyx, 421, 424.
Nilssonia, 421.
nogueyi, Cinixys, 397.

nogueyi, Homopus, 296, 397.
nogueyi, Kinixys, 397.
nogueyi, Kinixys b., 166, 383, 388, **396-399**, *380*, *381*.
normalis, Cyclanosteus s., 444.
Notochelys, 188.
novemcostatum, Tortisternum, 422.
novemcostatus, Coelognathus, 422.
nuttalli, Amblyomma, 248, 293, 393.
nyassensis, Caelatura, 466.
Ocadia, 186, 187, 188.
oceanica, Cephalochelys, 489, 491.
oculifer, Psammobates, 168, 300-303, 314, **315-319**, 321, 329, 332, 360, 362, *313*, *317*.
oculifera, Chersinella, 316.
oculifera, Clemmys, 316.
oculifera, Emys, 316.
oculifera, Psammobates, 316.
oculifera, Testudo, 299, 301, 315, 326.
officinalis Gomphopelta, 421.
oligotylus, Cyclanorbis, 167, 437, 438, 443.
olivacea, Caouana, 495.
olivacea, Caretta, 495.
olivacea, Caretta c., 496.
olivacea, Chelonia, 494, 495.
olivacea, Lepidochelys, 494.
olivacea, Lepidochelys o., 471, **495-498**.
olivacea, Thalassochelys, 495.
Onychochelys, 484.
Onychochelys kraussi, 484, 486.
Ophisops (as Ophiops), 275.
orangensis, Chersinella f., 301, 326.
orbicularis, Emys, 167, 170, 184, 188, 189, 191, 201, **202-209**, *190*, *205*, *206*, *212*, *214*, *217*.
orbicularis, Emys o., 204.
orbicularis, Testudo, 201, 202.
Orlitia, 187.
ornata, Trionyx, 421.
Ornithodorus moubata, 332.
oscarboettgeri, Testudo, 301, 326, 329.
Oscaria, 421.
Oscaria swinhoei, 421.
Oxyuridae, 332.
pallida, Testudo a., 368.
pardalis, Geochelone, 224, 227, 238, 251, 254, 255.
pardalis, Geochelone p., 228-230, 250, **251-254**.
pardalis, Megachersine, 238.
pardalis, Testudo, 221, 235, 251.
pardalis, Testudo p., 238, 251.
peersi, Pseudomopus s., 360.
peguensis, Trionyx, 421.
pelasgorum, Chelonia, 490.
Pelochelys, 414.
Pelochelys bibronii, 415.
Pelodiscus, 421.
Pelodiscus triunguis, 426.
Peltastes, 254.
Peltastes geographicus, 321.
Peltastes geometricus, 321.
Peltastes leithii, 277.
Peltastes m. whitei, 264.
Peltastes semiserratus, 316.
Peltastes sulcatus, 231.
Peltastes tentorius, 337.
Peltastes verreauxii, 324.
Peltastes verroxii, 324.
Peltonia, 254.
Pelusios gabonensis, 453.
Pelusios niger, 453.
Pemphis ocidula, 481.
petersii, Cyclanorbis, 436, 443.
petersii, Cyclanosteus, 436, 443.
petersii, Cycloderma, 443.
piscatella, Chersinella t., 301, 337.
piscatella, Psammobates t., 337.
Placobdella jaegerskioeldi, 466.
planicauda, Acinixys, *217*

platynota, Geochelone, 226.
Platypeltis, 421.
Platysterninae, 181, **182.**
Platysternon, 181, 298.
Pleurodira, 163, 417.
polyaspis, Chelonia, 495.
polyphemus, Gopherus, 283.
porcata, Dermatochelys, 500.
Potamochelys, 421.
procterae, Malacochersus, 287, *285.*
procterae, Testudo, 287, 288, 289, 292.
Psammobates, 166, 218, 220, 221, 255, 259, **294-315**, 343, 344, 378.
Psammobates depressa, 301, 327, 329, 331.
Psammobates fiskii, 327.
Psammobates f. colesbergensis, 327.
Psammobates f. cronwrighti, 327.
Psammobates f. fiskii, 327.
Psammobates geometricus, 168, 174, 253, 291, 300-303, 314, 316, **319-324**, *313.*
Psammobates oculifer, 168, 300-303, 314, **315-319**, 321, 329, 332, 360, 362, *313*, *317.*
Psammobates oculifera, 316.
Psammobates tentoria, 337.
Psammobates tentorius, 300, *306*, *308.*
Psammobates t. albanica, 337.
Psammobates t. duerdeni, 338.
Psammobates t. karruica, 338.
Psammobates t. piscatella, 337.
Psammobates t. tentorioides, 337.
Psammobates t. tentorius, 301, 302, 309, 312, 313, 315, 316, 321, 327, **336-342**, *212*, *215*, *217*, *339*, *340.*
Psammobates t. trimeni, 301, 302, 309-311, 313, 315, 327, 330, **333-336**, 338, 342, *212.*
Psammobates trimeni, 333.
Psammobates t. verroxii, 289, 295, 301-303, 313, 314, 316, **324-333**, 336, 337, 338, 341, 342, 358, 362, *215*, *222*, *313*, *329.*
Psammobia vespertina, 494.
Psammodromus, 275.
Pseudemys, 186, 187, 189.
pseudocaretta, Chelonia, 485.
Pseudomopus, 353, 355.
Pseudomopus boulengeri, 362.
Pseudomopus signatus, 360.
Pseudomopus s. peersi, 360.
pseudomydas, Chelonia, 485.
Pseudotestudo, 166, 218, 258, **276**
Pseudotestudo kleinmanni, 276.
Psilognathus, 421.
Psilognathus laevis, 421.
pulchella, Diosma, 323.
pulchella, Testudo, 202.
punctata, Testudo, 191.
punctularia, Geoemyda, 350.
pusilla, Chersine, 345.
pusilla, Testudo, 262, 265, 345, 346, 368.
Pyxis, 218, 256, 259, 296, 297, 343, 376, 377.
Pyxis arachnoides, 259, 364, *217.*
radiata, Geochelone, 224, 255.
Rafetus, 421.
remivaga, Caretta, 495.
Remora remora, 480, 502.
remora, Remora, 480, 502.
renicapite, Astrorchis, 501.
reticularia, Deirochelys, 184, 188, 189.
rivulata, Clemmys c., 192.
rostrata, Caretta, 486.
rotunda, Testudo, 202.
rodolfianus, Trionyx t., 426.
ruppellii, Caouana, 495.
Sacalia, 191.
Sagittarius serpentarius, 351, 373.
Salsola, 282.
schlegelii, Dermochelys c., 500.

schlegelii, Sphargis c., 500.
schoensis, Kinixys, 387.
schoepfi, Testudo, 230, 405.
schonlandi, Chersinella, 301, 307, 309, 310, 311, 312, 326, 329.
scutella, Emys, 353.
scutella Testudo, 354.
Sedum, 273.
seimundi, Chersinella f., 326.
seimundi, Testudo, 301, 326, 329, 330.
semiserrata, Testudo, 299, 301, 316, 319.
semiserratus, Peltastes, 316.
senegalensis, Cryptopus, 443.
senegalensis, Cyclanorbis, 417-420, 436-439, **443-450**, 451, *419, 445, 447*.
senegalensis, Cyclanosteus, 438, 443.
senegalense, Cyeloderma, 443.
senegalensis, Emyda, 443.
senegalensis, Geochelone, 231.
senegalensis, Testudo r., 231.
septemcostata, Coptopelta, 422.
serpentarius, Sagittarius, 351, 373.
Seytina, 499.
Siebenrockiella, 187, 298.
signata, Chersine, 360.
signata, Testudo, 352, 353, 359.
signata Testudo C., 360.
signatae, Lorica t., 359.
signatus, Chersobius, 360.
signatus, Homopus, 168, 173, 237, 316, 353-357, **359-362**, 369, 378, *217, 357, 358*.
signatus, Pseudomopus, 360.
signatus, Testudo, 369.
sigriz, Clemmys, 193.
sigriz, Clemmys c., 195.
sigriz, Emys, 193.
sigriz, Terrapene, 193.
simpsoni, Mutela, 466.
Sinaspideretes, 412.
sinensis, Trionyx, 415, 417, 421, 422, 427.
Sinohadrianus, 219.
smithi, Chersinella v., 327.
smithi, Testudo, 299, 301, 325, 327, 329, 330, 333.
sordidus, Lanistes, 466.
spekei, Kinixys b., 388.
spekii, Kinixys, 379, 380, 387, 391.
Sphargis, 499.
Sphargis angusta, 500.
Sphargis coriacea, 500.
Sphargis c. schlegelii, 500.
Sphargis mercuralis, 499.
spinifer, Trionyx, 417, 421.
Spiroxys contortus, 199.
squamata, Eretmochelys, 485.
squamosa, Caretta, 485.
squamosa, Eretmochelys i., 486.
steindachneri, Trionyx, 417.
stellata, Testudo, 221, 225.
Stigmochelys, 221.
strauchi, Chersinella, 321.
strauchi, Testudo, 299, 301, 302, 321-323.
Stylemys 218, 255, 256, 343, 355.
Stylemys nebrascensis, 256.
subplana, Amyda, 422.
subplana, Dogania, 415.
subplanus, Trionyx, 415, 421, 427.
subsulcata, Chersinella t. 301 337.
sulcata, Geochelone, 168, 225-229, **230-235**, 241, 247, 369, *226, 232*.
sulcata, Testudo, 221, 230, 232, 237.
sulcatus, Centrochelys (P.), 231.
sulcatus, Peltastes, 231.
sumeiri, Aldabrachelys, 225.
sumeiri, Geochelone, 225, 259.
swinhoei, Oscaria, 421.
swinhoei, Trionyx, 417.
syriacum, Hyalomma, 273.
tarapacana, Thalassochelys, 491.

tarapacona, Thalassiochelys, 491.
Temnognathus, 421.
Temnognathus mordax, 421.
tentoria, Chersinella, 337.
tentoria, Psammobates, 337.
tentoria, Testudo, 301, 308, 309, 325, 336, 338, 339.
tentoria, Testudo g., 301, 321.
tentorioides, Chersinella t., 301, 337.
tentorioides, Psammobates t., 337.
tentorius complex, 309.
tentorius, Peltastes, 337.
tentorius, Psammobates, *306*, *308*.
tentorius, Psammobates t., 301, 302, 309, 312, 313, 315, 316, 321, 327, **336-342**, *212*, *215*, *217*, *339*, *340*.
tenuis, Chelonia, 475.
Terrapene, 183, 188.
Terrapene sigriz, 193.
tessellatus, Natator, 475.
Testudinella, 254.
Testudinidae, 180, **181**, 182.
Testudininae, 182, **209-221**, 256, 375, *210*.
Testudo, 172, 218, 220, 221, **254-261**, 284, 295, 298, 343, 344, 354, 364, 375, 376, 378.
Testudo africana, 368, 369.
Testudo angulata, 342, 345, 346.
Testudo arcuata, 499.
Testudo areolata, 352, 367, 369, 387.
Testudo a. pallida, 368.
Testudo armata, 251.
Testudo bellii, 346.
Testudo bergeri, 326.
Testudo biguttata, 229, 250, 251.
Testudo bipunctata, 229, 251.
Testudo boettgeri, 299, 301, 326, 327, 329, 330, 332.
Testudo cafra, 360.
Testudo calcarata, 228, 231, 238, 241.
Testudo campanulata, 264, 277.
Testudo (C.) angulata, 346.
Testudo caouana, 490.
Testudo caretta, 470, 489, 490.
Testudo cartilaginea, 421.
Testudo caspica, 191.
Testudo C. cafra, 360.
Testudo C. signata, 360.
Testudo capediana, **474**
Testudo cephalo, 489, 490.
Testudo comptoni, 218, 354.
Testudo coriacea, 499.
Testudo denticulata, 404.
Testudo elegans, 221, 225.
Testudo erosa, 374, 404.
Testudo euphratica, 421.
Testudo europaea, 201, 202.
Testudo fasciata, 369.
Testudo ferox, 421.
Testudo fiski, 301, 325, 327, 329, 331.
Testudo flava, 202.
Testudo geometrica, 173, 294, 299, 301, 316, 319, 337, 387.
Testudo g. nigriventris, 301, 337.
Testudo g. tentoria, 301, 321.
Testudo gigantea, 225, 255.
Testudo graeca, 170, 218, 254-259, 261, 276, 282, 298, 299.
Testudo g. bettai, 265.
Testudo g. floweri, 259, 260.
Testudo g. graeca, 259, 260, **261-276**, *212*, *214*, *217*, *257 266*, *267*.
Testudo g. ibera, 259, 265.
Testudo g. mauritanica, 264.
Testudo guttata, 191.
Testudo hermanni, 170, 258, 260, 281, *212*, *257*, *281*.
Testudo horsfieldi, 254, 258, 283.
Testudo ibera, 170, 262, 265.
Testudo imbricata, 484, 485.

Testudo insculpta, 191.
Testudo japonica, 474.
Testudo kleinmanni, 218, 220, 258-261, 264, **276-283**, *212*, *214*, *278*, *279*, *280*.
Testudo leithii, 218, 276, 277, 280.
Testudo loveridgii, 287-290, 292, 387.
Testudo lutaria, 202.
Testudo luteola, 253, 299, 301, 321, 323.
Testudo lyra, 499.
Testudo macropus, 474.
Testudo m. amboinensis, 319.
Testudo marginata, 173, 254, 258, 261, 262, 264, 276, 282.
Testudo marina, 474.
Testudo mauritanica, 262.
Testudo meleagris, 202.
Testudo miniata, 368, 369.
Testudo minuta, 323.
Testudo muhlenbergii, 191.
Testudo mydas, 473, 474.
Testudo nasicornis, 490.
Testudo oculifera, 299, 301, 315, 326.
Testudo orbicularis, 202.
Testudo oscarboettgeri, 301, 326, 329.
Testudo pardalis, 221, 235, 251.
Testudo p. pardalis, 251.
Testudo procterae, 287, 288, 289, 292.
Testudo pulchella, 202.
Testudo punctata, 191.
Testudo pusilla, 262, 265, 345, 346, 368.
Testudo radiata, 255.
Testudo r. senegalensis, 231.
Testudo schoepfii, 230, 405.
Testudo scutella, 354.
Testudo seimundi, 301, 326, 329, 330.
Testudo semiserrata, 299, 301, 316, 319.
Testudo signata, 352, 353, 359.
Testudo signatus, 369.
Testudo smithi, 299, 301, 325, 327, 329, 330, 333.
Testudo stellata, 221, 225.
Testudo strauchi, 299, 301, 302, 321, 322, 323.
Testudo sulcata, 221, 230, 232, 237.
Testudo t. africana, 345, 346.
Testudo tentoria, 301, 308, 325, 336, 338, 339.
Testudo t. fiskii, 326, 333.
Testudo tornieri, 283, 286, 288.
Testudo (M.) tornieri, 287.
Testudo trimeni, 301, 307-311, 333.
Testudo triunguis, 420, 421, 423.
Testudo tuberculata, 499.
Testudo verreauxii, 324, 327, 337.
Testudo verroxii, 301, 324, 327.
Testudo v. bergeri, 327.
Testudo viridis, 473, 474.
Testudo viridis-squamosa, 474.
Testudo vulgaris, 474.
Testudo whitei, 264.
tetradactyla, Chersine, 368.
Tetrathyra, 436.
Tetrathyra baikii, 438, 439, 443, 444.
Tetrathyra vaillantii, 444.
Thalassiochelys tarapacona, 491.
Thalassochelys, 470, 489.
Thalassochelys caretta, 491, 495.
Thalassochelys caouana, 489.
Thalassochelys controversa, 495.
Thalassochelys corticata, 491, 492.
Thalassochelys olivacea, 495.
Thalassochelys tarapacana, 491.
thunbergii, Caretta, 474.
Tilapia, 433.
tornieri, Malacochersus, 167, 172, 284, **286-294**, 378, 388, *212*, *214*,

217 257, 285, 288.
tornieri, Testudo, 283, 286, 288.
tornieri, Testudo (M.), 287.
Tortisternum, 422.
Tortisternum novemcostatum, 422.
trimeni, Chersinella, 333.
trimeni, Psammobates, 333.
trimeni, Psammobates t., 301, 302, 309-311, 313, 315, 327, 330, **333-336**, 338, 342, *213.*
trimeni, Testudo, 301, 307-311, 333.
Trionychidae, 180, **412-420**, *416.*
Trionyx, 220, 414, **420-423**, 467, 470.
Trionyx aegyptiacus, 420, 422, 423.
Trionyx cariniferus, 421.
Trionyx cartilagineus, 415.
Trionyx emoryi, 417.
Trionyx euphraticus, 417.
Trionyx ferox, 417.
Trionyx formosus, 415, 421.
Trionyx gangeticus, 415, 422.
Trionyx hurum, 415.
Trionyx javanicus, 421.
Trionyx labiatus, 424, 427, 433, 434.
Trionyx leithii, 415.
Trionyx mortoni, 425.
Trionyx muticus, 417.
Trionyx nigricans, 415.
Trionyx niloticus, 421, 424.
Trionyx ornata, 421.
Trionyx peguensis, 421.
Trionyx sinensis, 415, 417, 421, 422.
Trionyx spinifer, 417, 421.
Trionyx steindachneri, 417.
Trionyx subplanus, 415, 421, 422, 427.
Trionyx swinhoei, 417.
Trionyx triunguis, 415, 417-419, **423-435**, *419, 428, 430, 431.*
Trionyx t. rudolfianus, 426.
Trionyx vertebralis, 427.
triunguis, Amyda, 426.
triunguis, Amyda t., 427.
triunguis, Pelodiscus, 426.
triunguis Testudo, 420, 421, 423.
triunguis, Trionyx, 415, 417-419, **423-435**, *419, 428, 430, 431.*
tuberculata, Testudo, 499.
Tyrse, 421.
Tyrse nilotica, 425.
uintensis, Geochelone, 224.
vaillantii, Tetrathyra, 444.
Venus verrucosa, 494.
verreauxii, Peltastes, 324.
verreauxii, Testudo, 324, 337.
verroxii Chersinella, 327.
verroxii, Peltastes, 324.
verroxii, Psammobates t., 289, 295, 301-303, 313, 314, 316, **324-333**, 336, 337, 338, 341, 342, 358, 362, *215, 222, 313, 329.*
verroxii, Testudo, 301, 324, 327.
verrucosa, Venus, 494.
vertebralis, Trionyx, 427.
vesperina, Psammobia, 494.
virgata, Chelone, 476.
virgata, Chelonia, 474.
viridis, Chelone, 475.
viridis, Chelonia, 474.
viridis, Mydas, 475.
viridis-squamosa, Testudo, 474.
viridis, Testudo, 473, 474.
vulgaris, Emys, 193.
vulgaris, Testudo, 474.
whitei, Peltastes m., 264.
whitei, Testudo, 264.
Xylocopa nigrita, 392.
yniphora, Asterochelys, 224.
yniphora, Geochelone, 342.
youngi, Kinixys, 388.
Yuen, 421.
Yuen leprosus, 421.
Zizyphus jujuba, 275.
zombensis, Kinixys, 388.
zombensis, Kinixys b., 387.
zuluensis, Kinixys, 388.
zuluensis, Kinixys b., 387.

PLATES

PLATE 1

Geochelone sulcata. (From Sowerby and Lear.)

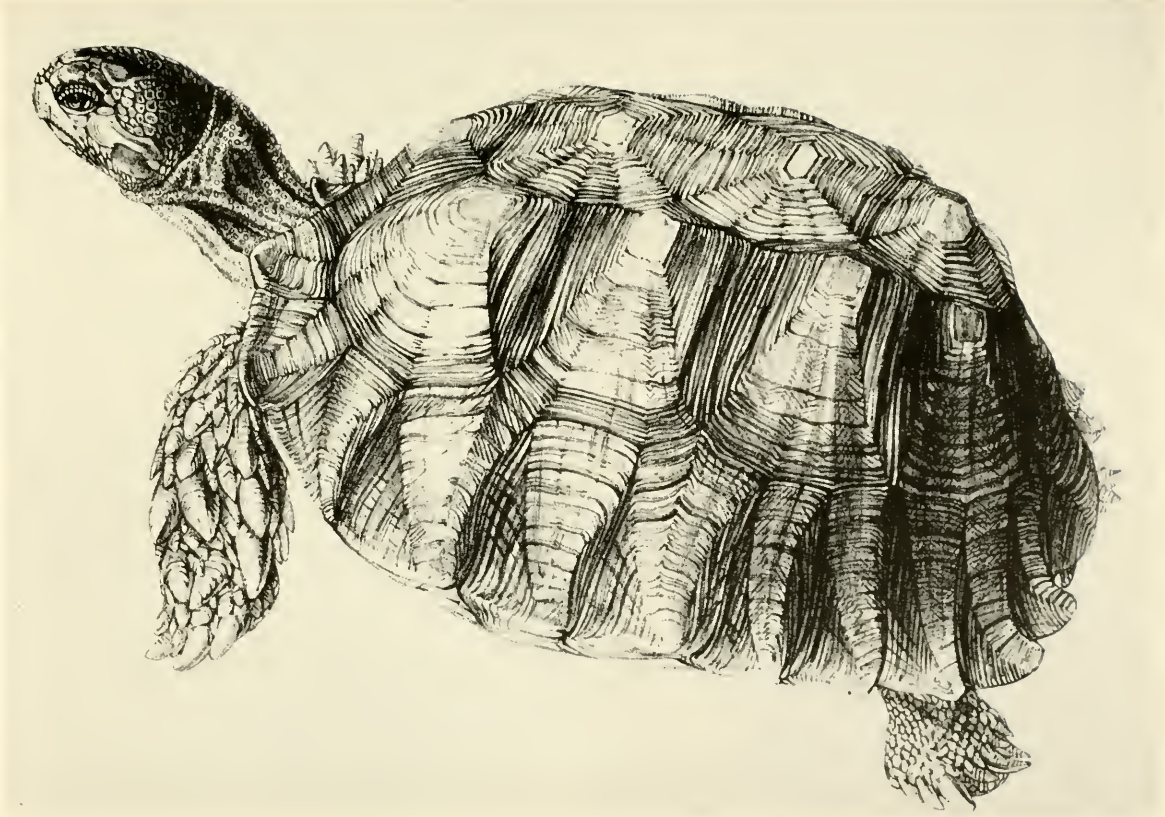


PLATE 1

PLATE 2

Geochelone pardalis subspecies

A. *G. p. pardalis* juv. (M.C.Z. 22473) ex Aroab, Southwest Africa.

B. *G. p. babcocki* juv. (M.C.Z. 40005) ex Mt. Mbololo, Kenya Colony.

C. *G. p. pardalis* adult (M.C.Z. 16713) ex Kolmanskop, Southwest Africa.

D. *G. p. babcocki* adult (M.C.Z. 18156) ex Arusha, Tanganyika Territory.

(Frank White, photographer.)

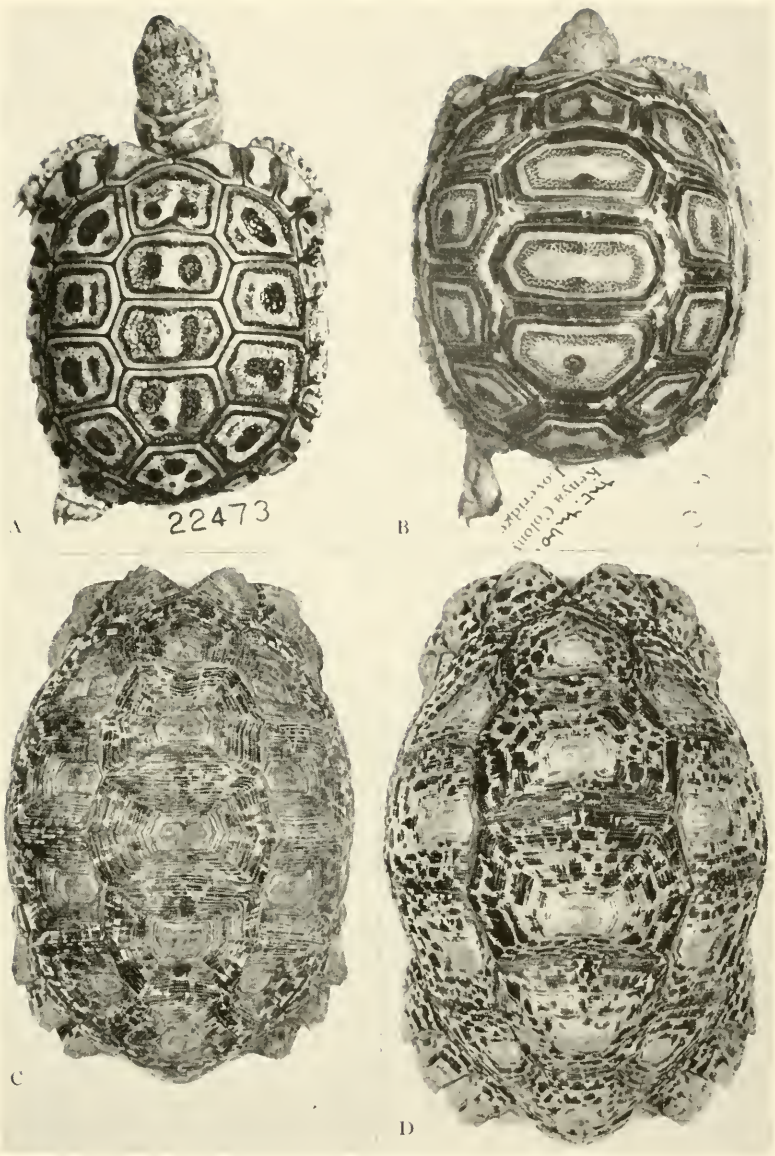


PLATE 2

PLATE 3

Testudo graeca graeca

Adult (M.C.Z. 29909) ex Mamora Forest, Rabat, Morocco. Dorsal and ventral views.

(Frank White, photographer.)

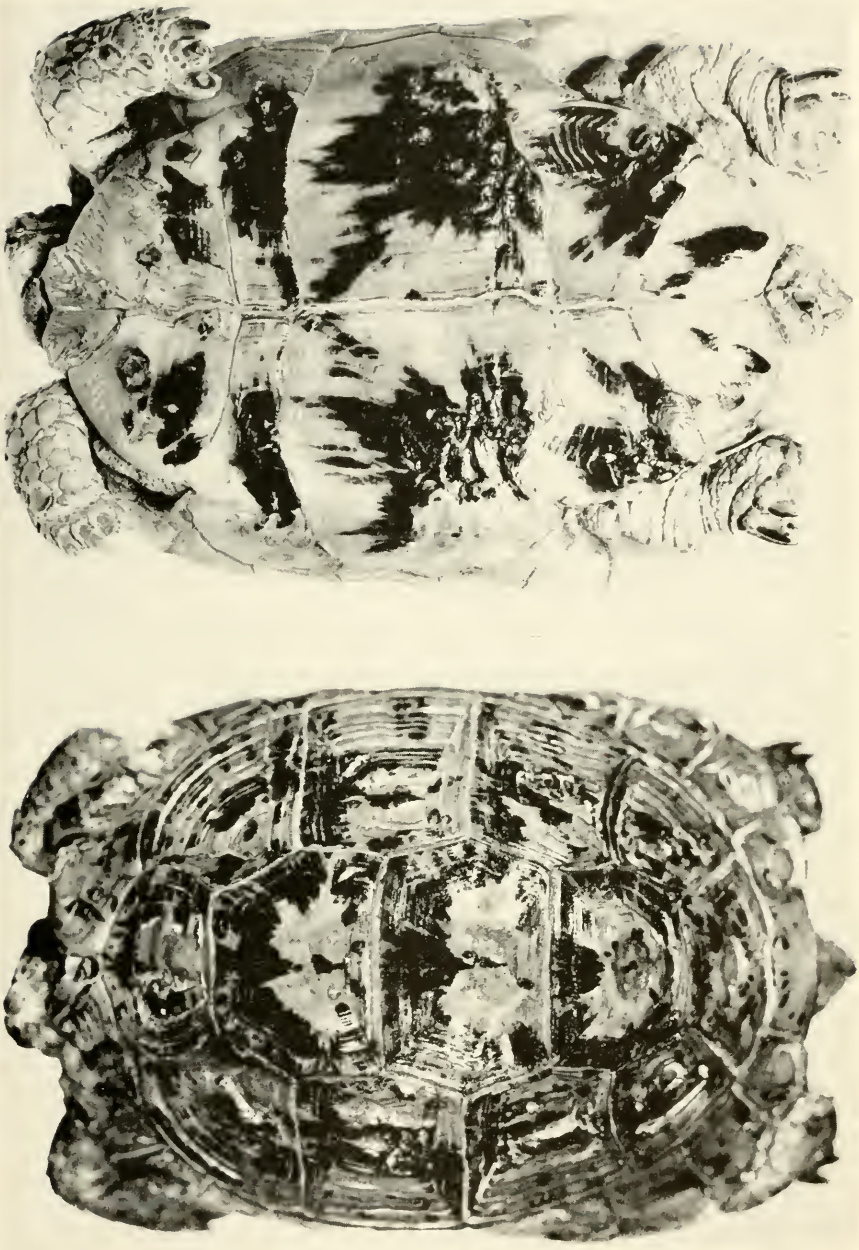


PLATE 3

PLATE 4

Testudo kleinmanni

Adult (M.C.Z. 54044) ex Salum, Western Desert, Egypt. Dorsal and ventral views.

(Frank White, photographer.)

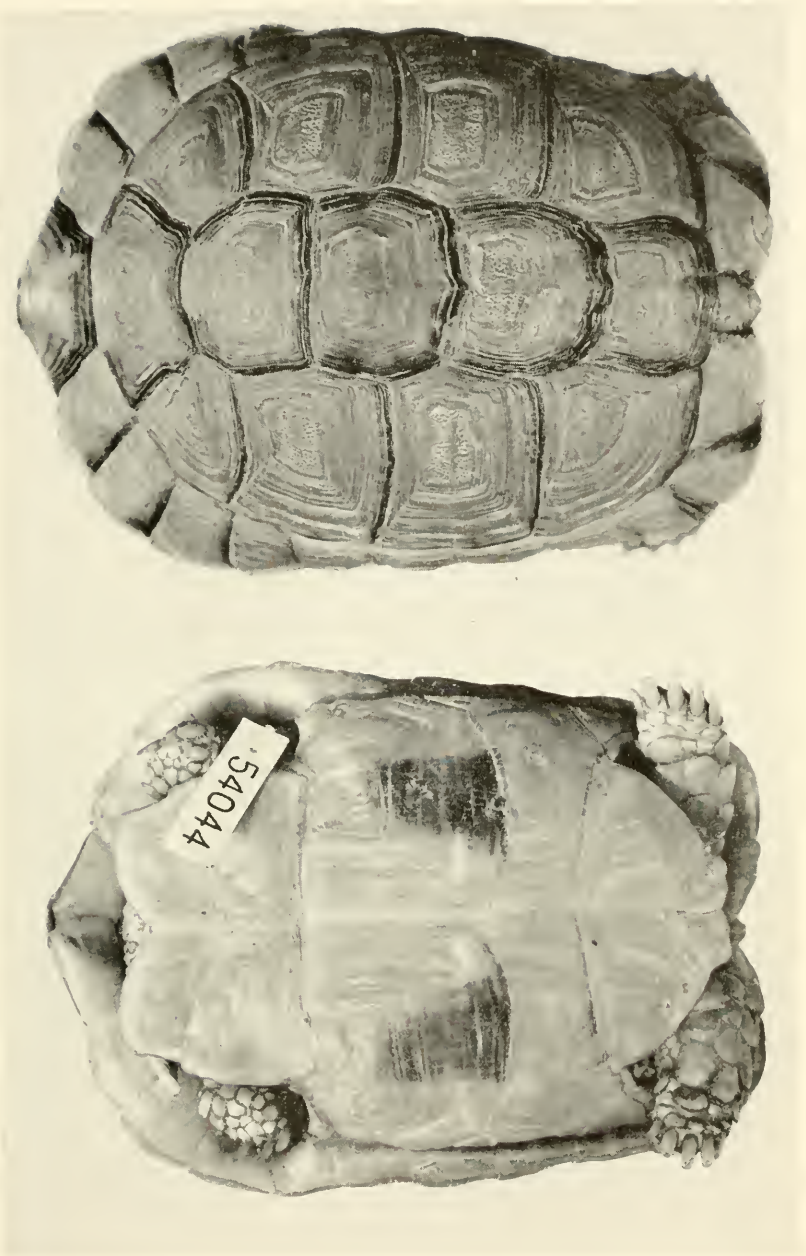


PLATE 4

PLATE 5

Malacochersus tornieri

Adult (M.C.Z. 30004) ex Mangasini, Usandawi, Tanganyika. Dorsal and ventral views.

(Frank White, photographer.)

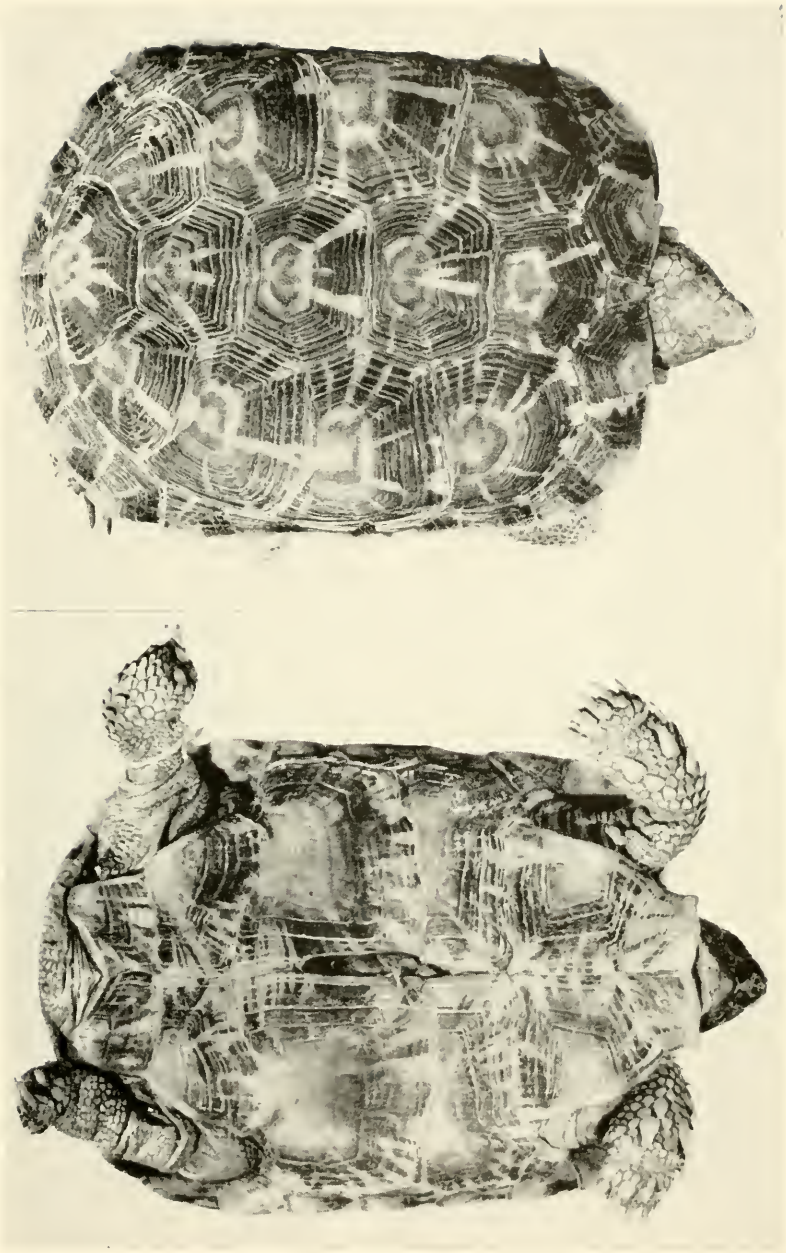


PLATE 5

PLATE 6

Malacochersus tornieri

Juvenile (Holotype of *procterae*, B.M. 1923.10.9.102 now 1946.1.22.59) ex Ikikuyu, south of Gulwe, Tanganyika.

B, C. Dorsal and ventral views; A. head and limbs enlarged.

(Courtesy of British Museum. Peter Green, photographer.)

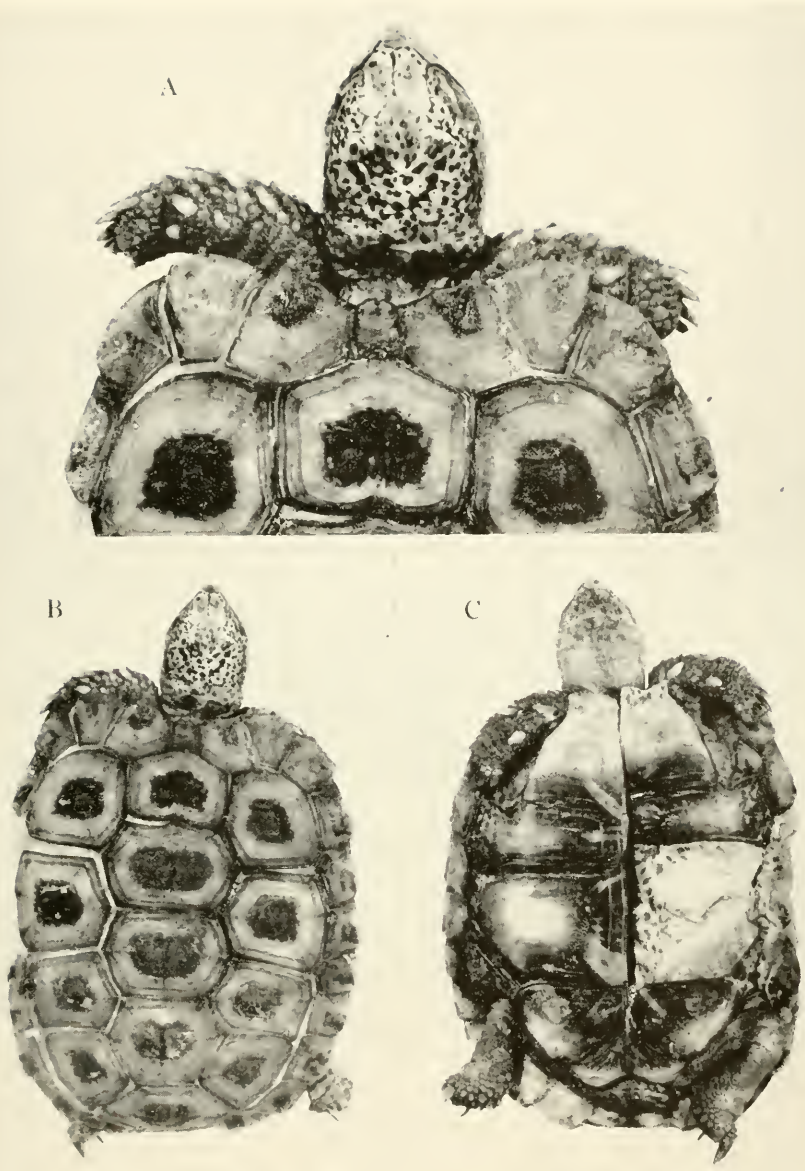


PLATE 6

PLATE 7

Psammobates oculifer

Adult (Type of *semiserrata*) ex "between Latakoo and the Tropic of Capricorn."

a, a. Nuchal shield and forelimb of *oculifer,* compared with

b, b. nuchal shield and forelimb of *geometricus.*

(From Andrew Smith.)

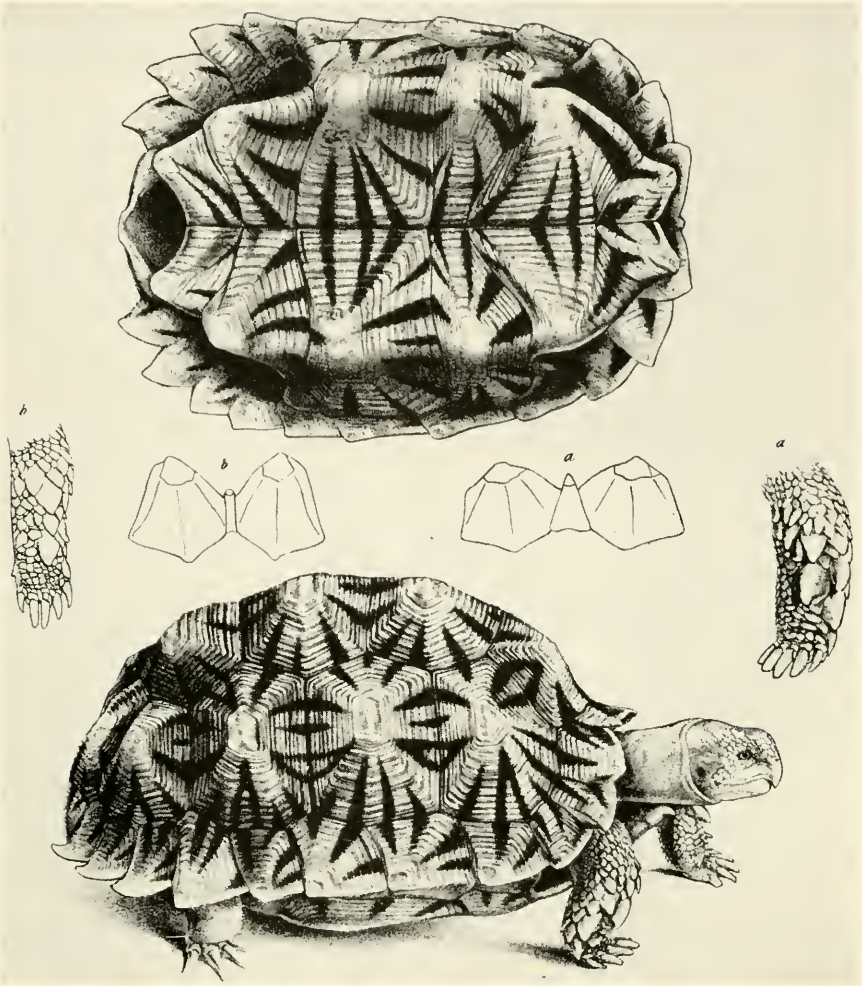


PLATE 7

PLATE 8

Psammobates geometricus

A, B. Juv. (*luteola* phase) (P.M.) ex "Cap".
(Frank White, photographer.)

C, D. Adult (B.M.) ex South Africa.
(Courtesy of British Museum. Peter Green, photographer.)

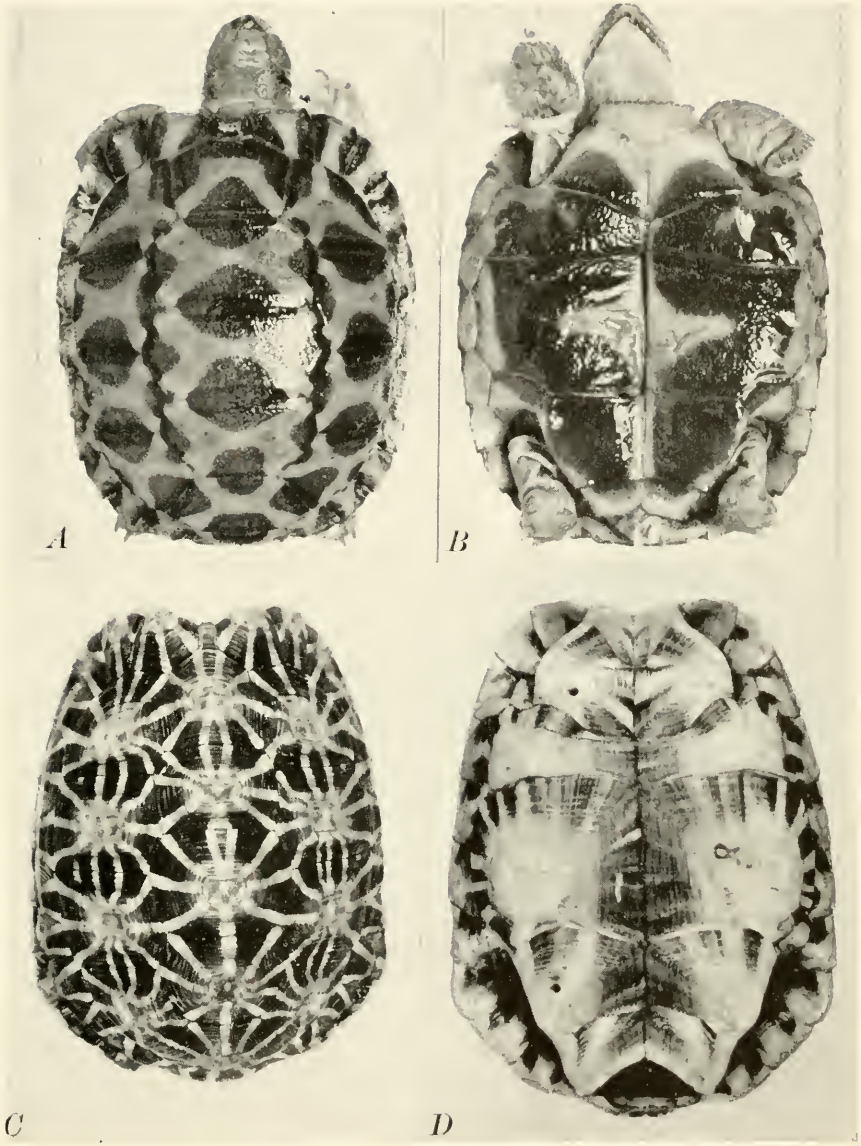


PLATE 8

PLATE 9

Psammobates tentorius verroxii

Adult (Type of *verroxii*) ex "near the sources of the Garriep or Orange River."

(From Andrew Smith.)

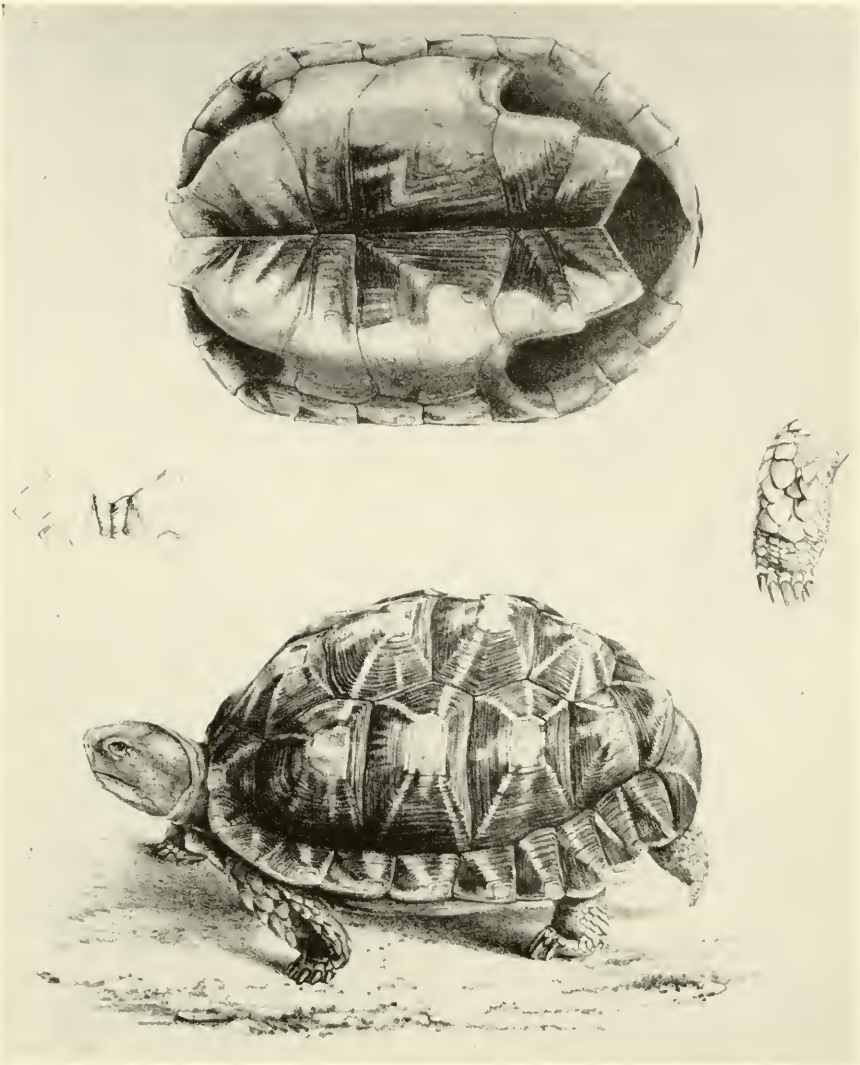


PLATE 9

PLATE 10

Psammobates tentorius subspecies: dorsal patterns.

A. *P. t. verroxii* Adult (Paratype of *schonlandi*. M.C.Z. 42222) ex Steinkopf, L. Namaqualand.

B. *P. t. verroxii* Adult (color form *bergeri* in B.M.) ex Barby, Tiraz Mtns., Southwest Africa.

C. *P. t. tentorius* Adult (typical pattern. M.C.Z.) ex "South Africa."

D. *P. t. tentorius* Adult (aberrant. M.C.Z. 46604) ex "South Africa."

(Frank White, photographer.)

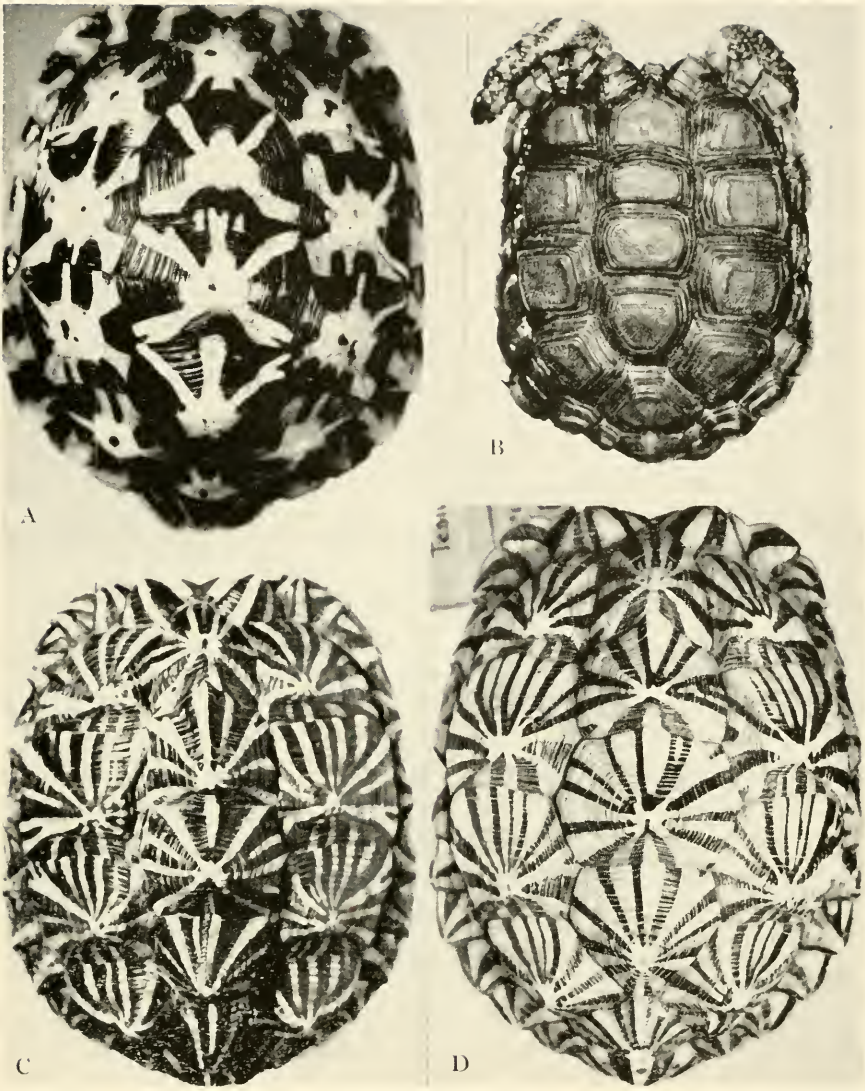


PLATE 10

PLATE 11

Psammobates tentorius tentorius

Plastral patterns of nine Transvaal Museum specimens from Matjesfontein, Cape Province.

A. T.M. 19537. B. T.M. 19650. C. T.M. 19497.
D. T.M. 19496. E. T.M. 19649. F. T.M. 19536.
G. T.M. 19480. H. T.M. 19479. I. T.M. 19495.

(Frank White, photographer.)

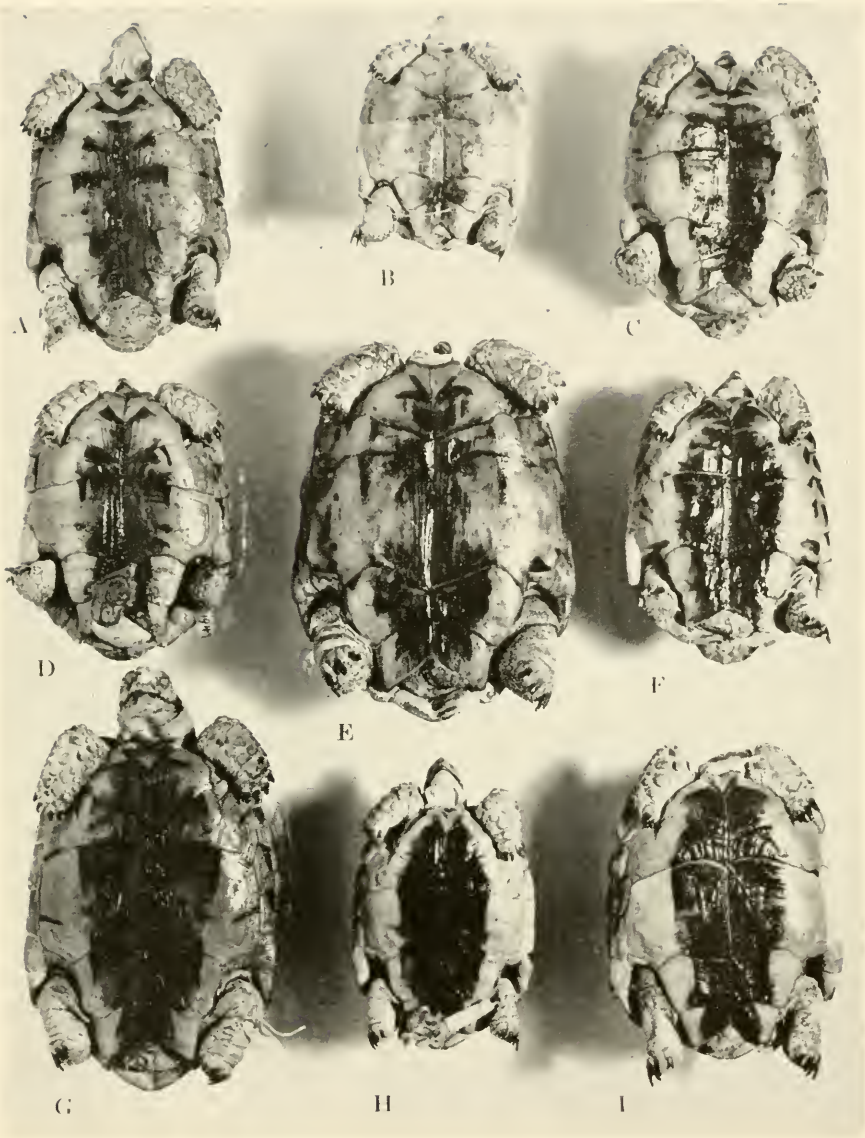


PLATE 11

PLATE 12

Chersina angulata ♂ and ♀

A. Dorsal view of strongly projecting gular in ♂.

A′. Plastral aspect of same.

B. Dorsal view of moderately projecting gular in ♀.

B′. Plastral aspect of same.

(From Vaillant.)

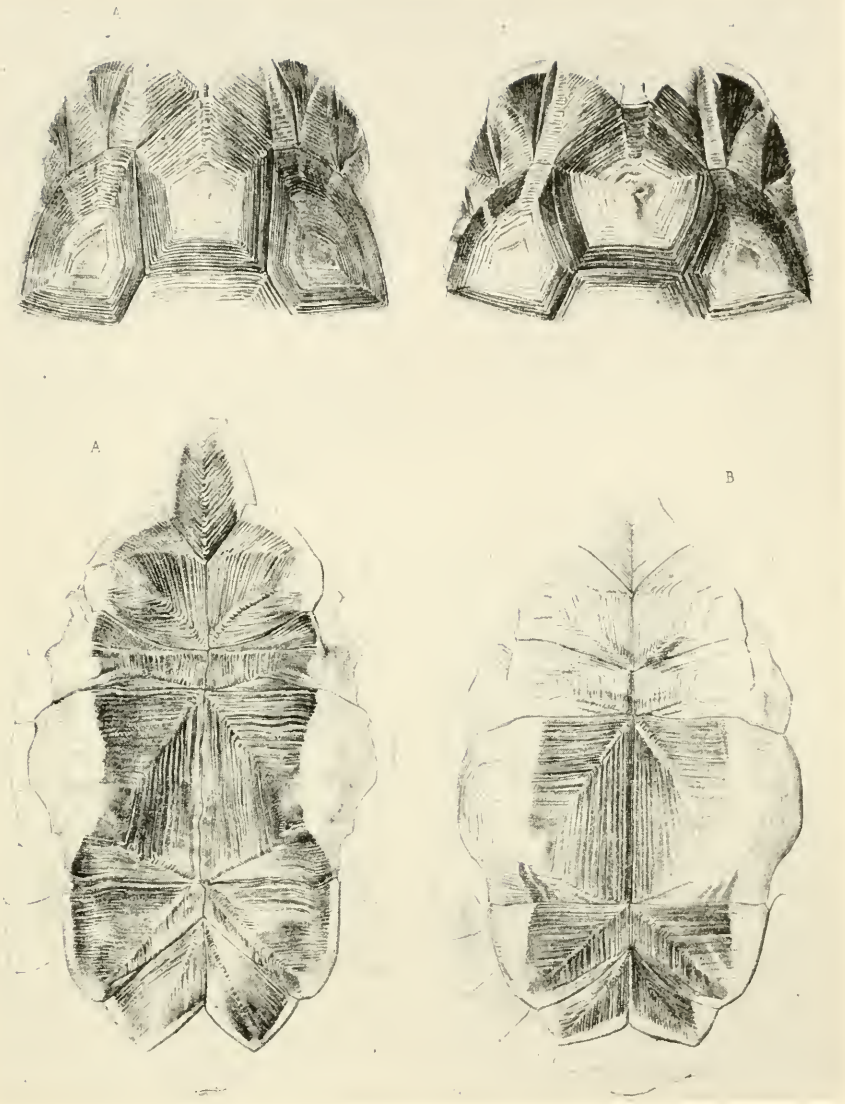


PLATE 12

PLATE 13

Homopus species: dorsal views of carapaces.

A. *H. signatus* (M.C.Z. 42218) ex Steinkop.

B. *H. boulengeri* (M.C.Z. 42231) ex "Cape Province."

C. *H. areolatus* (M.C.Z. 17525) ex Tootabi.

D. *H. femoralis* (M.C.Z. 17523) ex Hanovr.

(Frank White, photographer.)

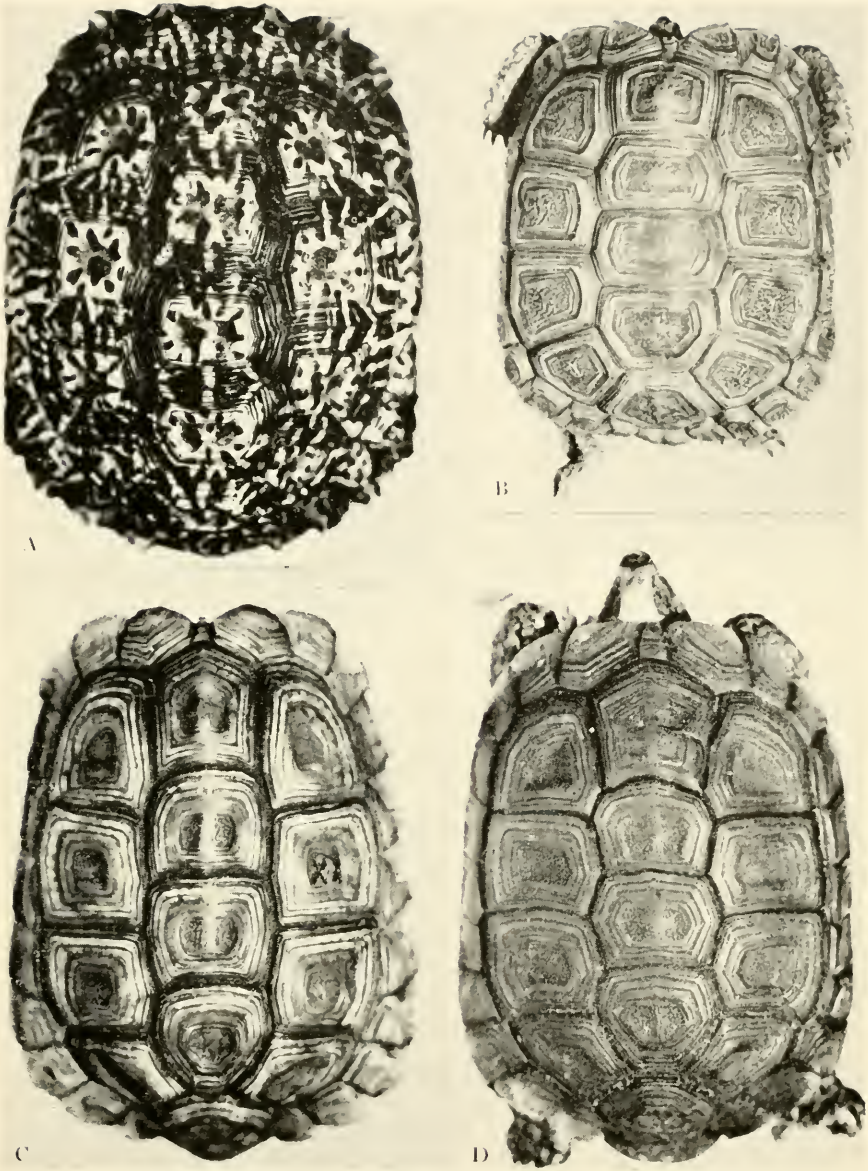


PLATE 13

PLATE 14

Kinixys species: dorsal views of carapaces.

A. *K. b. belliana* (M.C.Z. 42852) ex Lukafa, Belgian Congo.

B. *K. homeana* (M.C.Z. 38371) ex Ifan. Ondo, Nigeria.

C. *K. erosa* imm. (M.C.Z. 22486) ex Lenga, Liberia.

D. *K. b. belliana* (M.C.Z. 40015) ex Voi, Kenya Colony.

(Frank White, Photographer.)

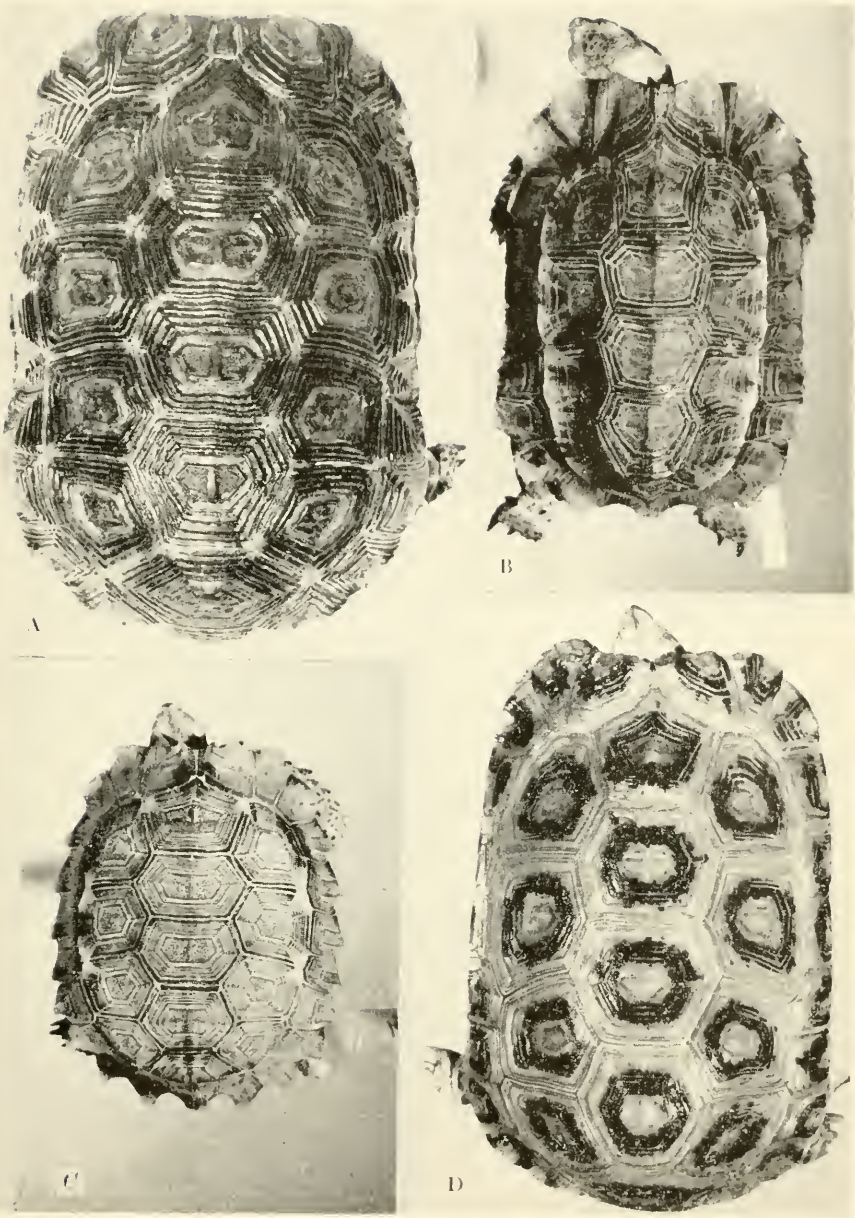


PLATE 14

PLATE 15

Trionyx triunguis
Juvenile ex Wadi Halfa, Nile, Egypt.

(From J. Anderson.)

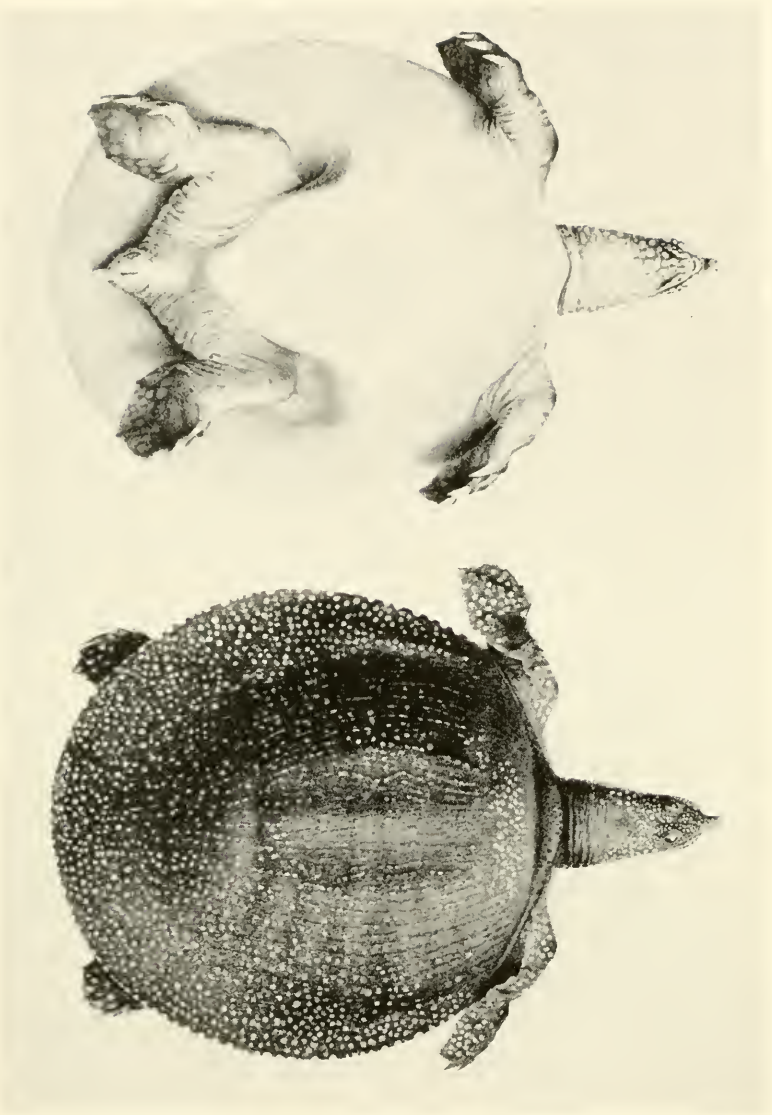


PLATE 15

PLATE 16

Cyclanorbis species: juveniles for comparison.

A. *C. elegans* (B.M. 1908.4.7.3) ex Anglo-Egyptian Sudan.

B. *C. elegans* same specimen, plastral view.

C. *C. senegalensis* (B.M. 1907.7.16.26) ex Gambia.

D. *C. senegalensis* same specimen, plastral view.

(Courtesy of British Museum. Peter Green, photographer.)

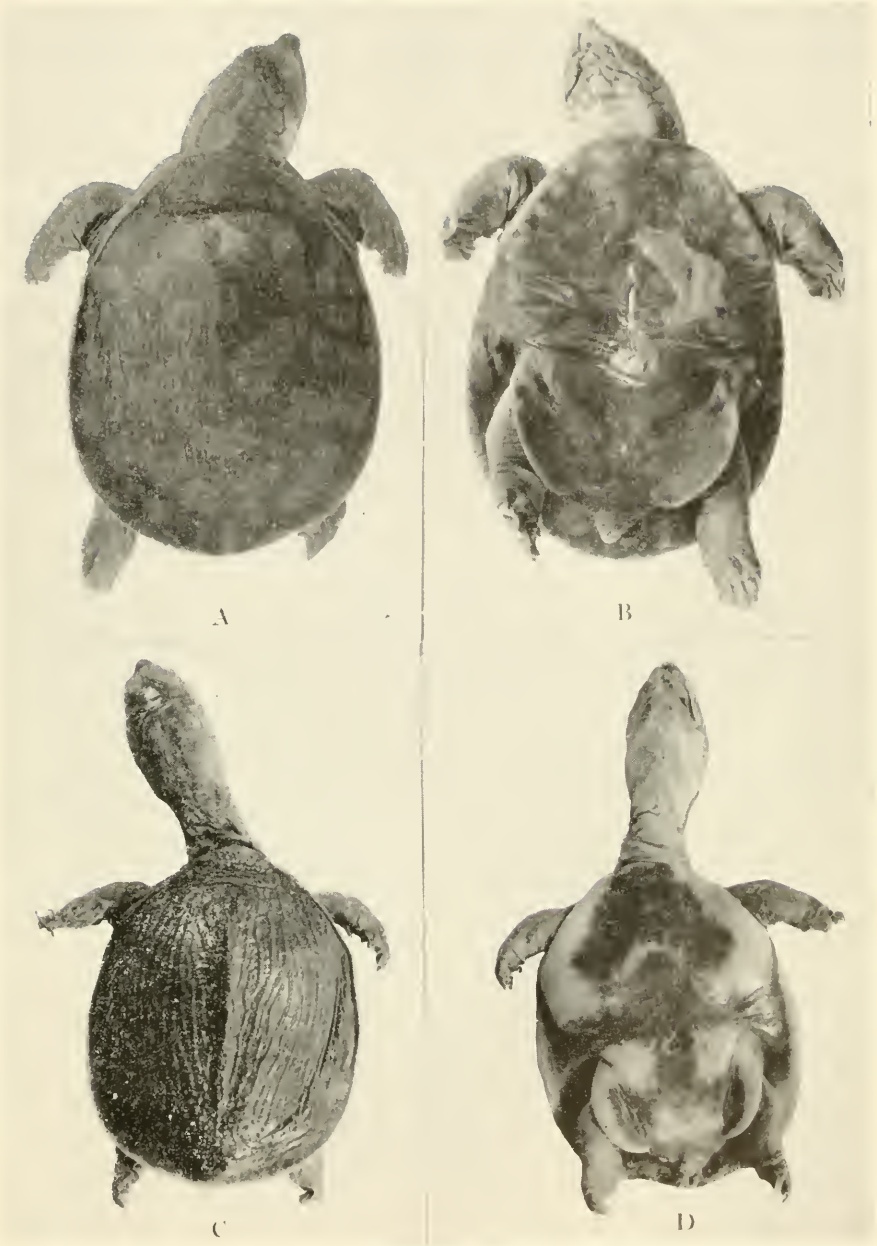


PLATE 16

PLATE 17

Cycloderma species: juveniles for comparison.

A. *C. frenatum* (M.C.Z. 50360) ex Chowe, Nyasaland.

B. Same specimen, plastral view.

(Frank White, photographer.)

C. *C. aubryi* (B.M. 1908.5.25.3) ex Zombo, Congo River, Belgian Congo.

D. Same specimen, plastral view.

(Courtesy of British Museum. Peter Green, photographer.)

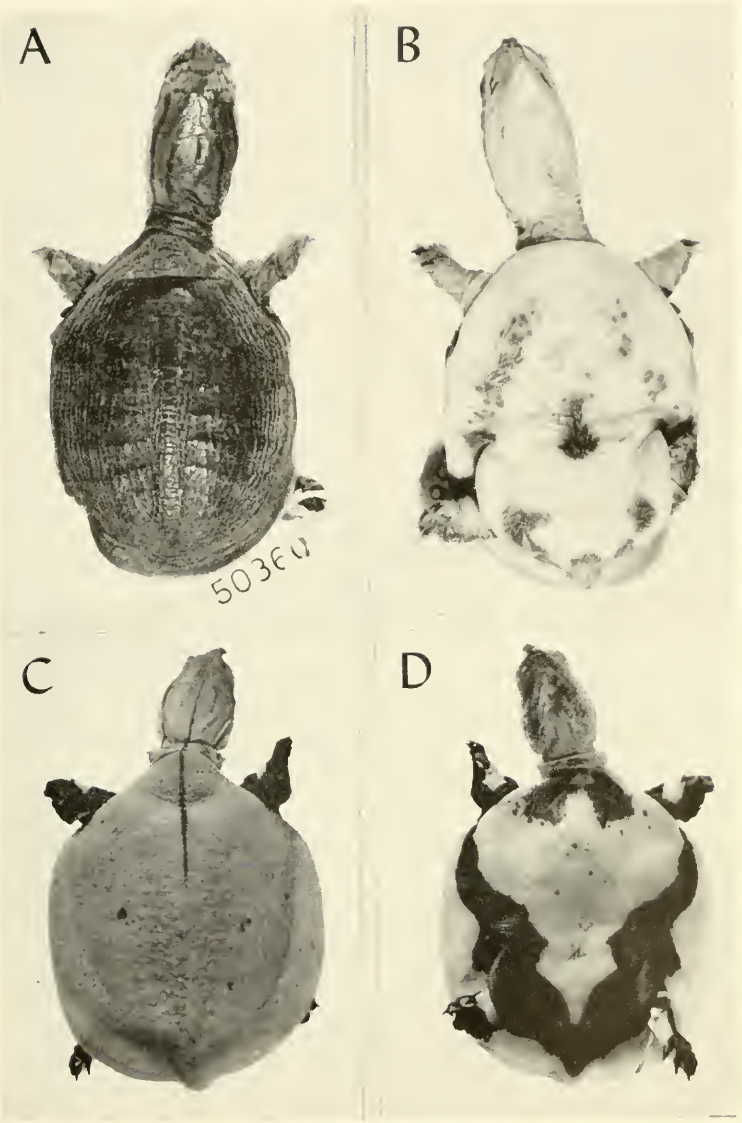


PLATE 17

PLATE 18

Cycloderma species: adults for comparison.

A. *C. aubryi* (Type: Paris Museum) ex Gabon, French Congo.
(Reduced. From A. Duméril.)

B. *C. frenatum* (Cotype: Z.M.U.) ex Zambezi River, Mozambique.
(From W. K. H. Peters.)

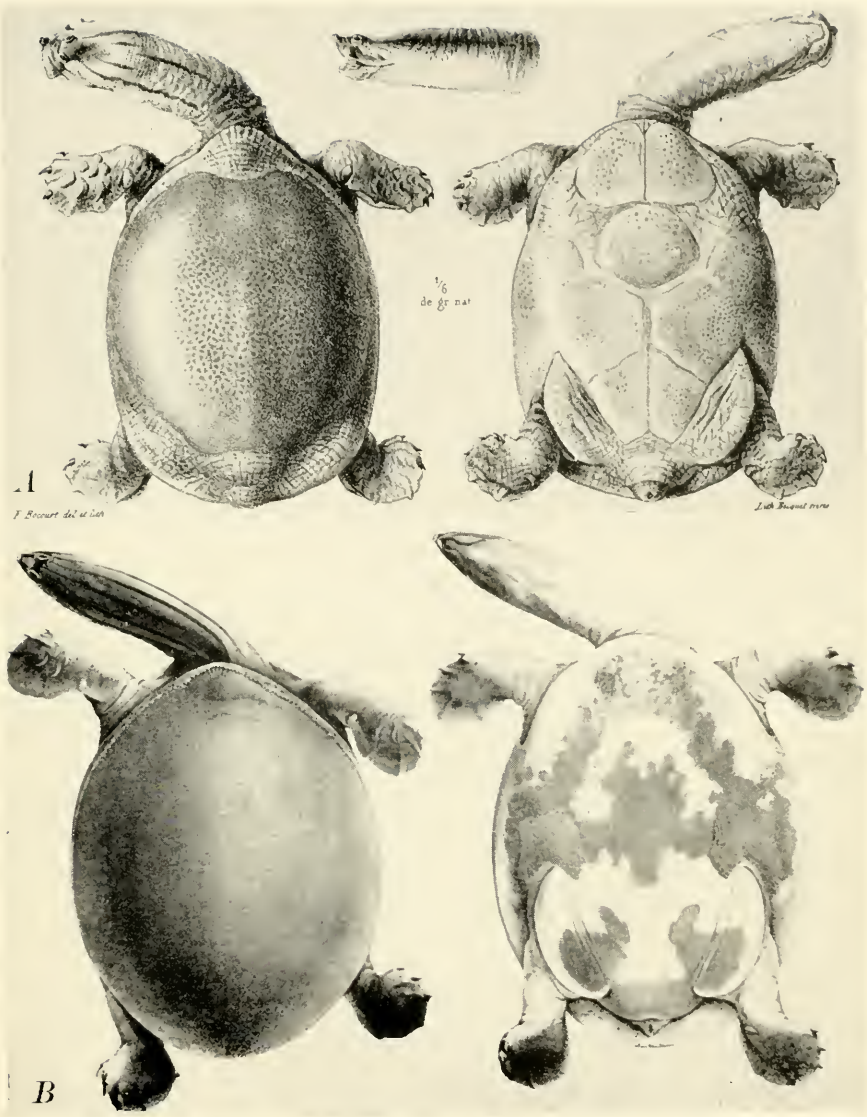


PLATE 18

Harvard MCZ Library
3 2044 066 303 876